

Comparative morphology and systematics of Brazilian Terebridae (Mollusca, Gastropoda, Conoidea), with descriptions of three new species

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ABSTRACT

A detailed morphological study is provided of the Brazilian Terebridae *Hastula cinerea* (Born, 1778), *H. hastata* (Gmelin, 1791), *Terebra brasiliensis* Smith, 1873, *T. crassireticula* n. nom. (replacing the junior homonym *T. reticulata* Simone & Verissimo, 1995), *T. gemmulata* Kiener, 1839, *T. leptapsis* n. sp., *T. taurina* (Lightfoot, 1786), and *T. spirosulcata* Simone & P. M. Costa n. sp. *Terebra sterigma* n. sp. is represented by shells only. Anatomically, the terebrids appear to be characterized by the reduction of the cephalic tentacles, the anterior extremity of the ctenidial vein being prominent and without gill filaments, and the rhynchodeal introvert and the anus being situated very posteriorly in the pallial cavity. The species of *Hastula* examined are characterized by an enlarged foot and by the complexity of the osphradium filaments. The species of *Terebra* examined are characterized by the eye situated at the tip of the tentacles, and also by a tendency for enlargement of the introvert, and reduction of the proboscis and the venom apparatus with their entire loss in some species (*T. gemmulata* and *T. brasiliensis*). The accessory proboscis structure is present in three of the *Terebra* species studied, and it is hypothesized that it may be a character of the family, as it is present in some *Hastula* species, and it may have been secondarily lost in several species of the family. Based on anatomical similarities, it is hypothesized that the conoidean proboscis is derived from a pleurembolic proboscis, homologous to the buccal mass part of this proboscis type, and the rhynchodeal wall is homologous to the remaining regions of the pleurembolic proboscis.

KEY WORDS

Gastropoda,
Terebridae,
anatomy,
systematics,
proboscis,
homology,
Brazil.

RÉSUMÉ

Anatomie comparée et taxinomie de Terebridae du Brésil (Mollusca, Gastropoda, Conoidea) ; description de trois espèces nouvelles.

Huit espèces de Terebridae du Brésil font l'objet d'une étude anatomique détaillée : *Hastula cinerea* (Born, 1778), *H. hastata* (Gmelin, 1791), *Terebra brasiliensis* Smith, 1873, *T. crassireticula* n. nom. (nom de remplacement pour *T. reticulata* Simone & Verissimo, 1995, invalide pour homonymie primaire), *T. gemmulata* Kiener, 1839, *T. leptapsis* n. sp., *T. taurina* (Lightfoot, 1786) et *T. spirosulcata* Simone & P. M. Costa n. sp. *Terebra sterigma* n. sp. est représenté uniquement par des coquilles vides. Au plan de leur anatomie, les Terebridae sont caractérisés par une réduction des tenracules céphaliques ; le vaisseau efférent de la branchie dont l'extrémité antérieure, proéminente, ne porte pas de filaments branchiaux ; l'introvers du rhynchodeum et l'anus situés très en arrière dans la cavité palléale. Les espèces d'*Hastula* examinées sont caractérisées par le développement du pied et la complexité des filaments de l'osphradium. Les espèces de *Terebra* sont caractérisées par la position des yeux à l'extrémité des tenracules, par une tendance au développement de l'introvers, et à la réduction du proboscis et de l'appareil à venin, allant jusqu'à leur disparition totale chez certaines espèces (*T. gemmulata* et *T. brasiliensis*). Des structures accessoires du proboscis sont présentes chez trois des espèces de *Terebra* étudiées, et il est possible qu'il s'agisse d'un caractère familial, car il est présent chez certaines *Hastula*, et peut avoir été secondairement perdu chez plusieurs autres espèces. En se fondant sur les similarités anatomiques, il est fait l'hypothèse que le proboscis des Conoidea dérive du proboscis de type pleurembolique et est homologue de la masse buccale des espèces possédant ce type de proboscis, la paroi du rhynchodeum étant homologue des autres parties du proboscis pleurembolique.

MOTS CLÉS

Gastropoda,
Terebridae,
anatomie,
systématique,
homologie,
proboscis,
Brésil.

INTRODUCTION

The Terebridae comprise more than 300 species in seas around the world (Bratcher & Cernohorsky 1987; Taylor 1990). They are easily differentiated from the other Conoidea by their elongated, multiwhorled shell. The systematics within the family has, however, been problematic, with most species still placed in the genus *Terebra* Bruguière, 1789 (Bratcher & Cernohorsky 1987).

The Brazilian Terebridae were revised by Matthews *et al.* (1975) who recognized seven species of *Terebra*: *T. taurina* (Lightfoot, 1786); *T. gemmulata* Kiener, 1839; *T. brasiliensis* (Smith, 1873); *T. concava* Say, 1822; *T. dislocata* Say, 1822; *T. protexta* (Conrad, 1846) and *T. doellojuradoi* Carcelles, 1953 and three of *Hastula* H. & A. Adams, 1853: *H. cinerea* (Born, 1778); *H. hastata* (Gmelin, 1791) and *H. salleana*

(Deshayes, 1859). Three more species have been described since: *T. riosi* Bratcher & Cernohorsky, 1985; *T. imitatrix* Auffenberg & Lee, 1988 (all present in Rios 1994) and *T. reticulata* Simone & Verissimo, 1995. An extensive anatomical description of a Brazilian terebrid is provided by Marcus & Marcus (1960) for *H. cinerea*, and brief data is provided in Auffenberg & Lee (1988) and in Simone & Verissimo (1995).

Taylor (1990) provided a complete and comprehensive history and commentary on the terebrids. He summarized the current informal (for systematics) classification of the terebrid foregut anatomy types (Ia, Ib, IIa, IIb, III) found in the literature (e.g., Miller 1971; Taylor & Miller 1990) with several interesting examples. The classification of the Conoidea (= Toxoglossa), as a whole, has also been analysed in some recent papers, of which Taylor, Kantor & Sysoev (1993) is considered the most important. This paper

discussed each foregut character, erected a uniform terminology, and concluded with a phylogenetic analysis of the superfamily based mainly on the shell, the operculum and foregut anatomy. Among the several conoideans analysed, the authors studied seven terebrids, giving as synapomorphies of the family the following characters: (1) rhynchodeal introvert; (2) accessory proboscis structure; (3) terebriform shell; (4) absence of an anal sinus in the shell aperture and (5) more than nine teleoconch whorls.

Although the foregut anatomy is fundamental for the understanding of the conoideans, and its characters have followed in importance that of the shell in systematics, it has obscured the importance of other structures such as the reproductive system and the mantle organs. Papers with anatomical data on structures other than the foregut are very few (e.g., Marcus & Marcus 1960).

This paper is part of a larger research project concerning the inter-relationship of some Caenogastropod groups, based mainly upon comparative morphology. Some Brazilian species of terebrids were selected for detailed morphological study with the following objectives: (1) to present a holistic morphological study of each species providing a basis for a discussion of several characters including and beyond those of the foregut and providing a basis for a future phylogenetic analysis of the family; (2) to establish the morphological characters of species from a geographic area from which they have been poorly studied, providing data for future revisions.

MATERIALS AND METHODS

A detailed list of the material examined follows each species description. Specimens largely belong to museum collections or were collected especially for this study. These collections are deposited in different institutions listed below (with other abbreviations) in Brazil and France. Several lots were obtained in following projects: (1) Marion-Dufresne Expedition "MD55"; (2) Integrated project "Coastal Rational Utilization of the Brazilian Tropical Region: São Paulo State", Instituto Oceanográfico da Universidade

de São Paulo (IOUSP); (3) "Oceanic Environmental Monitoring of the Campos Bay", IOUSP, GEOMAP, FUNDESPA.

The specimens were dissected by standard techniques, under a stereomicroscope; with the specimens immersed under water. The specimens were extracted from their shells by means of decalcification or the shells were broken. Serial sections of anterior regions were made by standard histological techniques, and stained with Mallory's triple stain. Some structures were also cleared in creosote after dehydration in an ethanol series and stained in carmine. Anatomical terminology follows Marcus & Marcus (1960) and for the foregut, Taylor *et al.* (1993).

ABBREVIATIONS USED IN THE FIGURES

aa	anterior aorta
ac	anterior extremity of ctenidial vein
ag	albumen gland
al	anal gland
an	anus
ap	accessory proboscis structure
as	accessory salivary gland
at	duct of accessory salivary gland
au	auricle
az	anal papilla
bd	venom bulb duct
bm	buccal mass
bs	blood sinus
bt	buccal tube
ca	capsule gland aperture
cc	chamber anterior to glandular tissue of capsule gland
cf	furrow formed by columellar fold
cg	capsule gland
ci	transverse muscle fibres
cm	columellar muscle
cv	ctenidial vein
dd	duct digestive gland
dg	digestive gland
ey	eye
ff	foot lateral furrow
fs	foot sole
ft	foot
gi	gill
gp	gonopericardial duct
he	haemocoelic cavity
hg	hypobranchial gland

ia	rhynchodeal introvert distal aperture or rhynchostome	rs	radular sac
ib	inner wall of buccal tube	rt	rectum
ig	ingesting gland	rw	rhynchodeal wall
il	inner layer of muscles of venom bulb	sd	salivary duct
in	intestine	sg	salivary gland
ip	insertion of introvert in foot muscles	si	siphon
kd	dorsal lobe of kidney	sn	snout
ki	kidney massive tissue	sp	siphon projections
km	membrane between kidney and pallial cavity	st	stomach
ks	ventral septate lobe of kidney attached to intestine	te	cephalic tentacles
lf	longitudinal muscle fibres	tg	tegument
m1	muscle uniting oesophagus with dorsal wall of haemocoel	tl	terminal pouch-like pad of male
m3	muscle connecting oesophagus with posterior extremity of rhynchodeal wall	tp	terminal pouch
mb	mantle border	ts	testis-seminal vesicle
mn	mantle notch	tt	radular tooth
mo	mouth	vb	venom bulb
mt	muscular tissue	vd	visceral vas deferens
ne	nephrostome	ve	ventricle
ng	nephridial gland	vg	venom gland
nr	nerve ring		
nv	nerve		
ob	outer wall of buccal tube		
oe	oesophagus		
oep	oesophageal pouch		
ol	outer layer of muscles of venom gland		
op	operculum		
os	osphradium		
ov	oviduct		
pb	proboscis		
pc	pericardium		
pd	penis duct		
pe	penis		
pf	pedal gland		
pg	anterior furrow of pedal glands		
ph	penis distal chamber		
pm	muscles in penis base		
pp	penis papilla		
ps	pallial sperm duct		
pt	prostate		
rc	receptaculum seminis		
re	rectal septum		
ri	rhynchodeal introvert		
rm	retractor muscle of proboscis		
ro	rhynchodeal introvert proximal aperture		

ABBREVIATIONS OF INSTITUTIONS

IBUFRJ	Instituto de Biologia, Universidade Federal do Rio de Janeiro, Brazil
MNHN	Muséum national d'Histoire naturelle, Paris, France
MNRJ	Museu Nacional da Universidade Federal do Rio de Janeiro, Brazil
MORG	Museu Oceanográfico da Fundação Universidade de Rio Grande, Brazil
MZSP	Museu de Zoologia da Universidade de São Paulo, Brazil

Genus *Hastula* H. & A. Adams, 1853

Hastula cinerea (Born, 1778)

(Figs 1A, B; 2; 3A; 4; 5; 6A, B; 7B; 8B)

Synonymy: cf. Matthews *et al.* (1975: 98) and Braicher & Cernohorsky (1987: 191).

Others: *Hastula cinerea* – Rios 1985: 131 (fig. 590). – Calvo 1987 (fig. 160). – Rios 1994: 181 (fig. 841).

MATERIAL EXAMINED. — **Alagoas**, Brazil, Maceió, Riacho Doce, 16.XII.1973, Menezes coll., 19 specimens (MZSP 25069).

Rio de Janeiro, Brazil, Cabo Frio, Conchas Beach, 6.I.1973, Marini coll., 6 specimens (MZSP 24673).

São Paulo, Brazil, Ubatuba, Tahatinga Beach, 8.I.1972, Marini coll., 23 specimens (MZSP

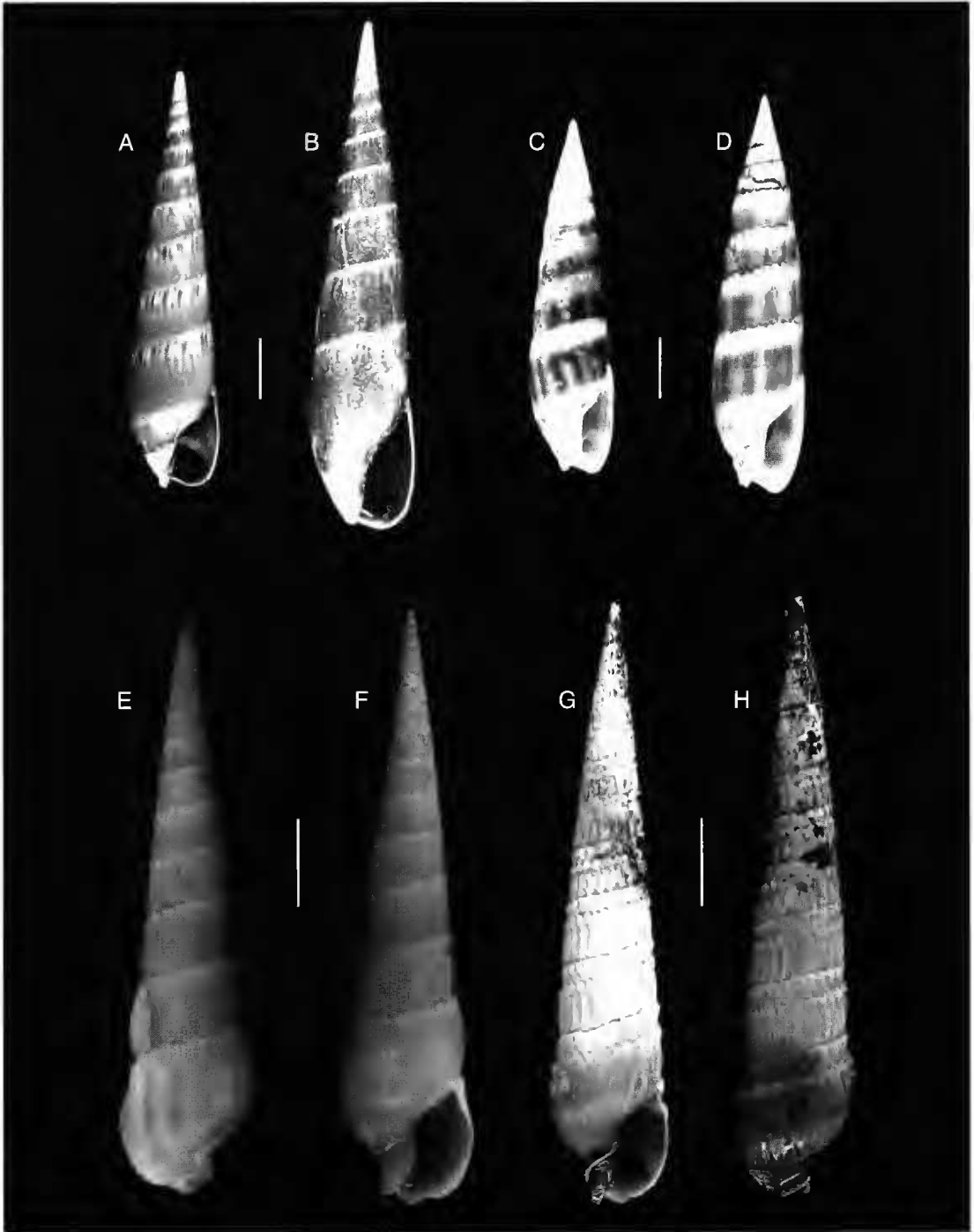


FIG. 1. — Shells; **A**, *Hastula cinerea*, normally pigmented shell; **B**, same species, melanic form; **C**, **D**, *Hastula hastata*, two specimens in frontal view; **E**, *Terebra spirosulcata* Simone & P. M. Costa n. sp., dorsal view of paratype MZSP 25213; **F**, same, frontal view; **G**, *Terebra gemmulata*, frontal view; **H**, same, dorsal view. Scale bars: **A**, **C**, **D**, **F**-**H**, 5 mm; **E**, **B**, 10 mm.

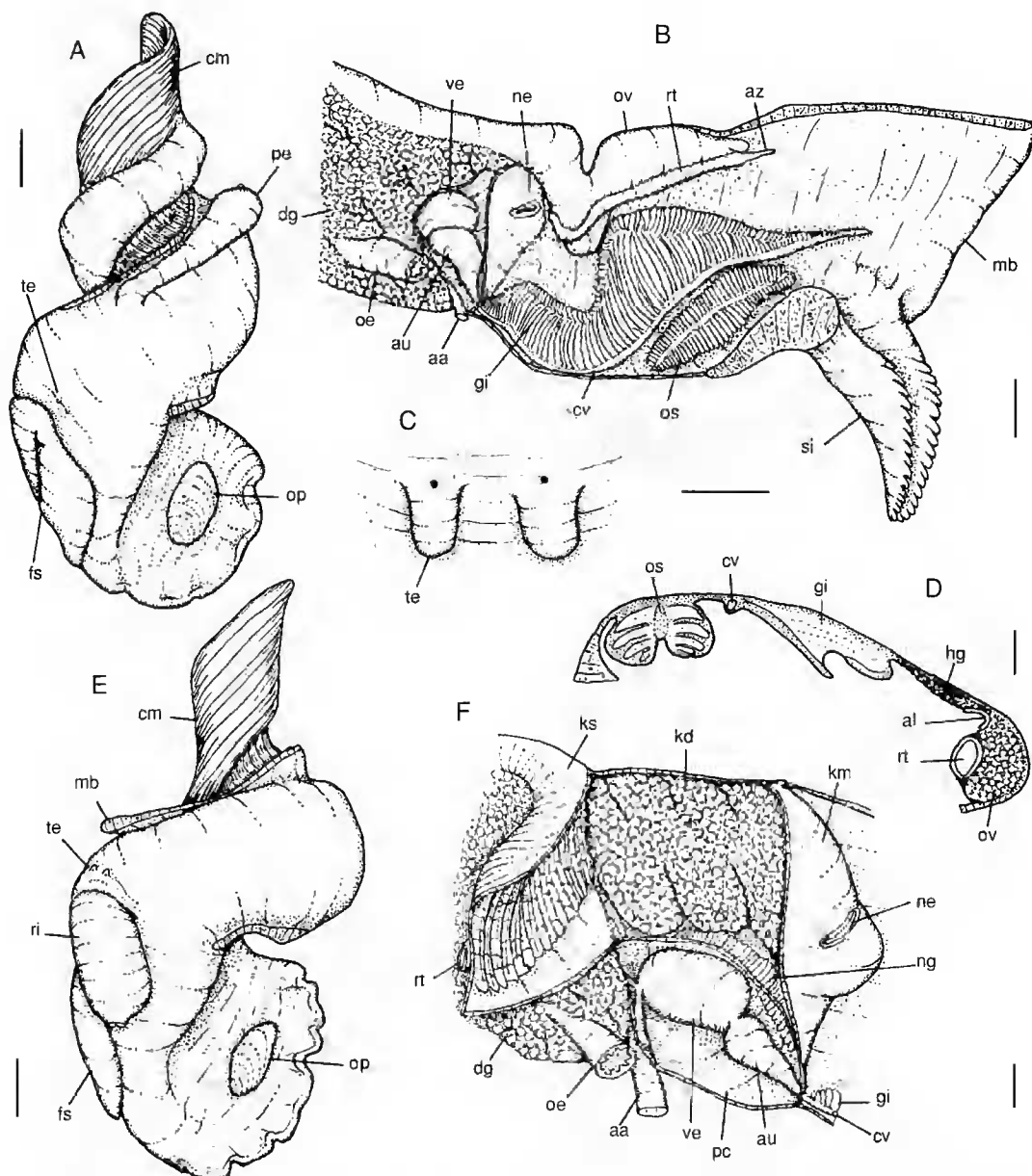


FIG. 2. — *Hastula cinerea*, anatomy; A, ♂ head-foot, mantle removed; B, mantle organs and anterior region of visceral mass, ventral-interior view; C, detail of 2A, tentacle region; D, transverse section of middle region of pallial cavity roof; E, ♀ head-foot with protracted introvert, mantle removed; F, anterior region of visceral mass with kidney and pericardium dissected and with interior structures exposed. Scale bars: 0.5 mm.

25083). — São Sebastião, Baraqueçaba Beach, 13.VII.1996, Simone coll., 1 specimen observed alive (MZSP 28599). — 26.X.1996, Simone coll., 1 specimen observed alive (MZSP 28600). — 16.V.1997, Simone coll., 4 specimens observed alive (MZSP

28605). — Guarujá, 20.IX.1968, Costa coll., 42 specimens (MZSP 25189).

DISTRIBUTION. — From Florida, USA, to Santa Catarina, Brazil.

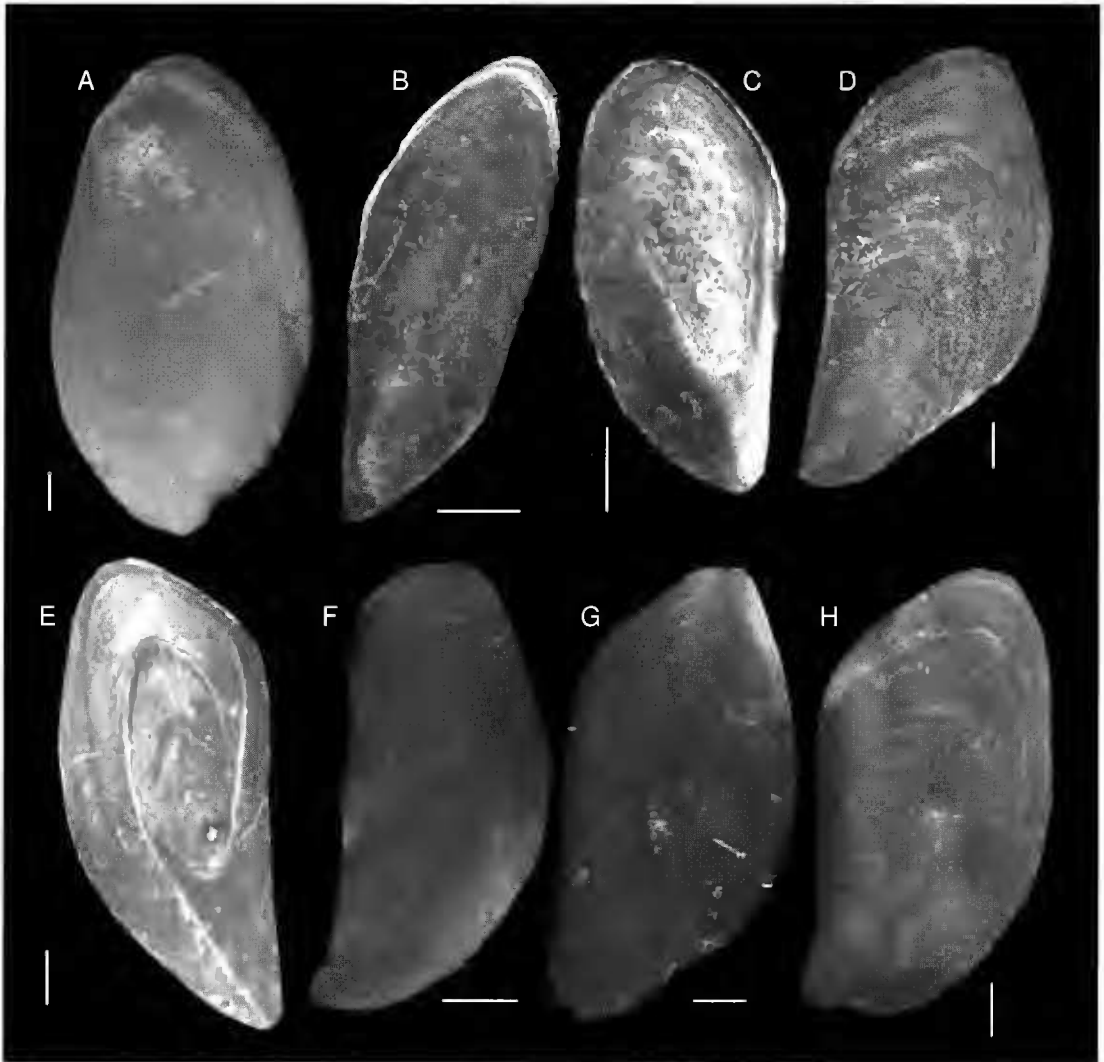


FIG. 3. — Opercula in SEM (outer view except those indicated); **A**, *Hastula cinerea*; **B**, *H. hastata*; **C**, same species, internal view; **D**, *Terebra gemmulata*; **E**, same species, internal view; **F**, *T. crassireticula*; **G**, *T. brasiliensis*; **H**, *T. spirosulcata*. Scale bars: **A**, **G**, 0.2 mm; **B-E**, **H**, 0.5 mm; **F**, 1 mm.

HABITAT. — Intertidal, sandy bottoms, beaches with waves of medium to high energy. Migrates during the tides using the extended foot to be carried shorewards by the wave and the sharp shell to anchor when the waves retreat.

DESCRIPTION

Shell (Fig. 1A, B)

A description of the shell can be found elsewhere (Marcus & Marcus, 1960: 27-28; Matthews

et al., 1975: 98-99, figs 29-31; Bratcher & Cernohorsky, 1987: 191-192, figs 233a-i). Melanic forms, i.e., with homogeneous dark brown shell, occur at a low frequency (Fig. 1B).

Head-foot (Fig. 2A, C, E)

Colour homogeneous cream, with pale gray spots on anterior structures. Head weakly differentiated from head-foot axis (Fig. 2A, E). Tentacles

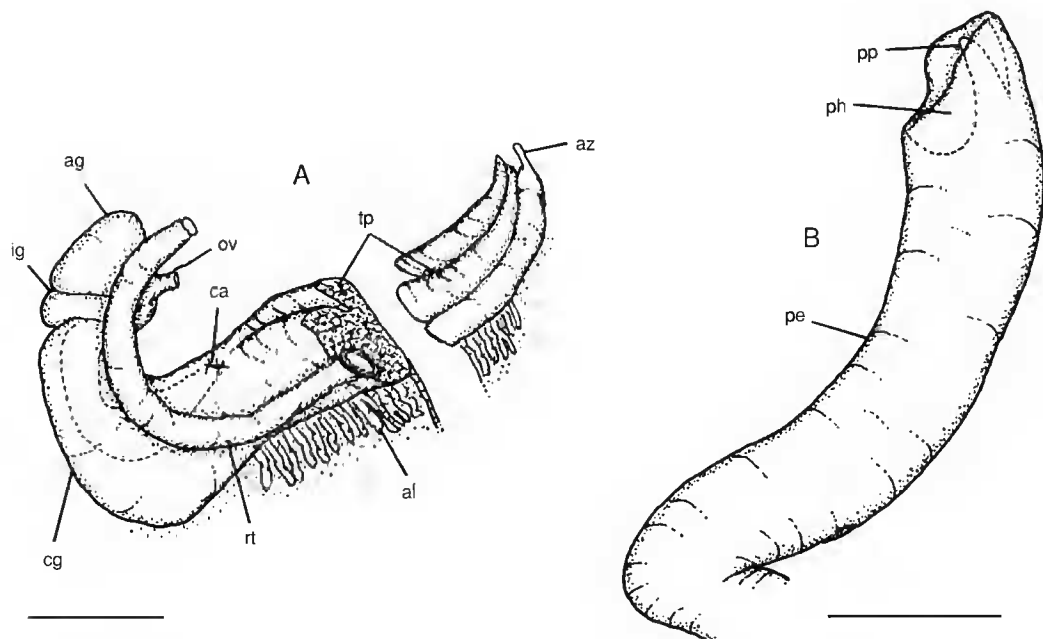


FIG. 4. — *Hastula cinerea*, anatomy. **A**, pallial oviduct, ventral view, including a transverse section of the anterior third; **B**, penis, ventral view. Scale bars: 1 mm.

very short, almost vestigial. Eyes very small, dark, located slightly below tentacle base (Fig. 2C). Basal, proximal introvert aperture rather broad, transverse, located anteriorly and ventral to tentacles. Foot large, occupying more than half a whorl, without clear divisions; sole with folded borders. Columellar muscle of about 1.5 whorl, rather thin. Other details in Marcus & Marcus (1960: 28-30).

Operculum (Figs 2A, E; 3A)

Minute, unguiculate, pale brown, located in middle region of posterodorsal foot surface, nucleus terminal (Figs 2A, E; 3A). Occupies small part of aperture.

Mantle organs (Figs 2B, D; 4A)

Mantle border simple, not pigmented. Siphon well-developed, pale cream, with borders entirely edged by small lobed papillae (Fig. 2B). Mantle cavity extends about two whorls. Osphradium bipectinate, elliptical, about one third of gill length; with several filaments uniform on both sides of osphradial ganglion; right filaments

similar in size to left filaments; each filament scalloped by about four decreasing digitations (Fig. 2D). Gill rather elliptical and long, about four fifths of pallial cavity length; anterior end rather far from mantle border; in anterior extremity only ctenidial vein present, in form of a small seprum (Fig. 2B; ac); filaments begin gradually at some distance from anterior end; each filament triangular, apex varies from central to located on the right, right margin varies from almost straight to convex; gill posterior extremity very close to pericardium. Ctenidial vein narrow and uniform all along its length, except for its broader anterior extremity. A proportionally broad space between gill and rectum. Hypobranchial gland thin, located in posterior half of cavity, at left of rectum, pale cream. Anal gland with some slender, irregular acina immersed in right margin of hypobranchial gland close to rectum (Fig. 4A), but not close to anus, purple. Pallial gonoducts run along right margin of posterior half of pallial cavity. Rectum narrow, lying ventral to and to left of pallial gonoducts. Anus close to anterior extremity of pallial oviduct in

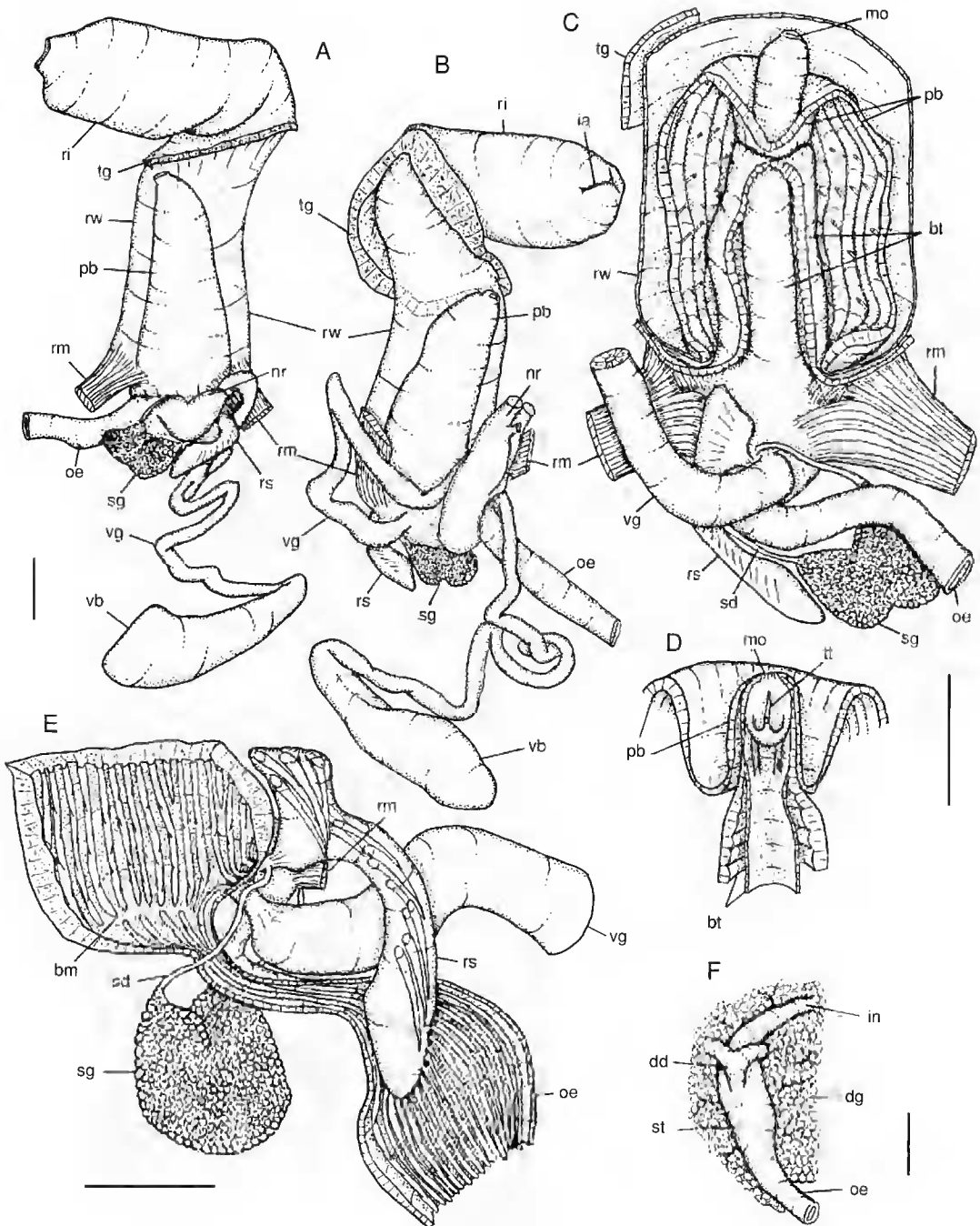


FIG. 5. — *Hastula cinerea*, anatomy; **A**, foregut removed from head-foot, dorsal view; **B**, same, ventral view; **C**, rhynchoideal wall, proboscis and buccal tube partially opened longitudinally, ventral view; **D**, detail of apical extremity of proboscis opened longitudinally, showing gripping of tooth; **E**, buccal mass and oesophagus opened longitudinally, internal surface exposed; **F**, stomach, ventral view, digestive gland partially removed. Scale bars: 1 mm.

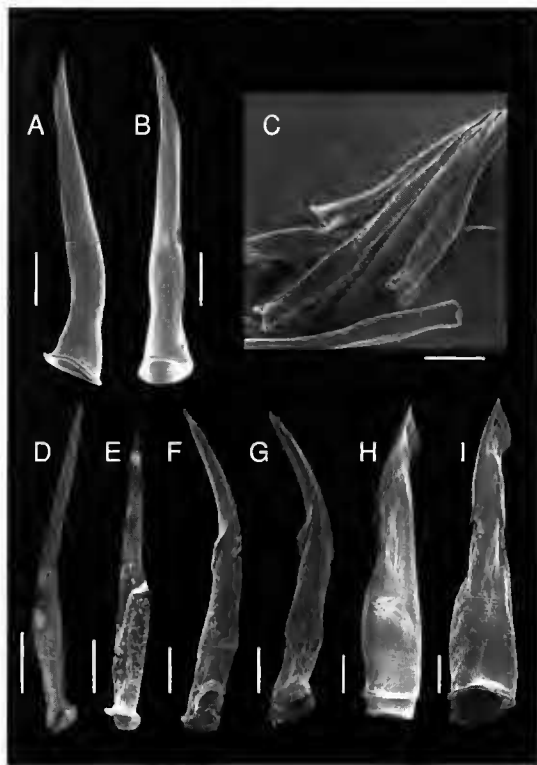


FIG. 6. — Radular teeth, SEM; A, B, *Hastula cinerea*; C, *Terebra crassireticula*; D, E, *H. hastata*; F, G, *T. taurina*; H, I, *T. spirosulcata*. Scale bars: A, B, F, G, 100 µm; C, 40 µm; D, E, 20 µm; H, I, 50 µm.

females or prostate in males; bearing a small, ventral papilla on its border (Figs 2B, 4A). Anterior half of pallial right margin without inner structures. Other details in Marcus & Marcus (1960: 30-32).

Circulatory and excretory systems (Fig. 2B, F)

Heart of medium size, located in left region of posterior limit of pallial cavity. Auricle just behind end of gill and anterior to ventricle. Aortas run along anterior surface of digestive gland. Kidney occupies almost half a whorl, flattened, located in right region of posterior limit of pallial cavity. Kidney with two main glandular masses, separated by a flattened chamber (Fig. 2F). Dorsal glandular mass thick (kd), clear brown, bulging into pallial cavity. Ventral glandular mass (ks) bordering rectum, pale cream,

bearing several, uniform transverse septa. Nephridial gland pale cream, triangular in section, bordering dorsal margin of membrane between kidney and pericardial chambers (ng). Nephrostome a transverse slit in middle region of membrane between kidney and pallial cavity. Other details in Marcus & Marcus (1960: 33-34).

Digestive system (Figs 2E; 5; 6A, B; 7B; 8B)

Rhynchodeal introvert occupies about half of remainder of foregut length, cylindrical (Figs 2E; 5A, B); muscular walls thick, composed of two closely connected muscular layers. Distal aperture of rhynchodeal introvert (rhynchostome) a small longitudinal slit, preceded by a thick sphincter. Inner rhynchodeal wall very thin, transparent (Fig. 5A, B), covering inner surface of anterior half of haemocoel, connected to it by small muscle fibres mainly located near rhynchostome. Proboscis conical, of about same length as rhynchocoel, muscular and thick (Fig. 5A-C); its base fused with that of rhynchodeal wall. A pair of large retractor muscles originate in mid-lateral region of inner surface of haemocoel and are inserted at rhynchodeal wall-proboscis transition, with a small part also inserted into buccal mass (Fig. 5C). Buccal mass spherical, with a long, broad buccal tube (Fig. 5C). Buccal tube with two muscular walls, connected with each other only at anterior extremity near mouth. Several small transverse muscle fibres connecting inner surface of proboscis wall with outer surface of outer buccal tube. Outer buccal tube wall thick, bearing mainly transverse muscle fibres. Inner buccal tube wall thin, semi-transparent, bearing mainly longitudinal muscle fibres, most of its inner surface smooth, with a few longitudinal folds. Anterior extremity of buccal tube, where it grips radular tooth, with a horseshoe-shaped inner fold (concavity anterior), with two posterior, longitudinal, muscular projections attached to dorsal surface, and a central, short, digitiform projection notching radular tooth base (Fig. 5D) (see also Marcus & Marcus 1960: fig. 7). Posterior extremity of outer buccal tube wall contours proboscis base, connected with it throughout its entire circumference by a thin layer of muscle fibres (Fig. 5C), but not fused with each other; buccal tube also inserting in

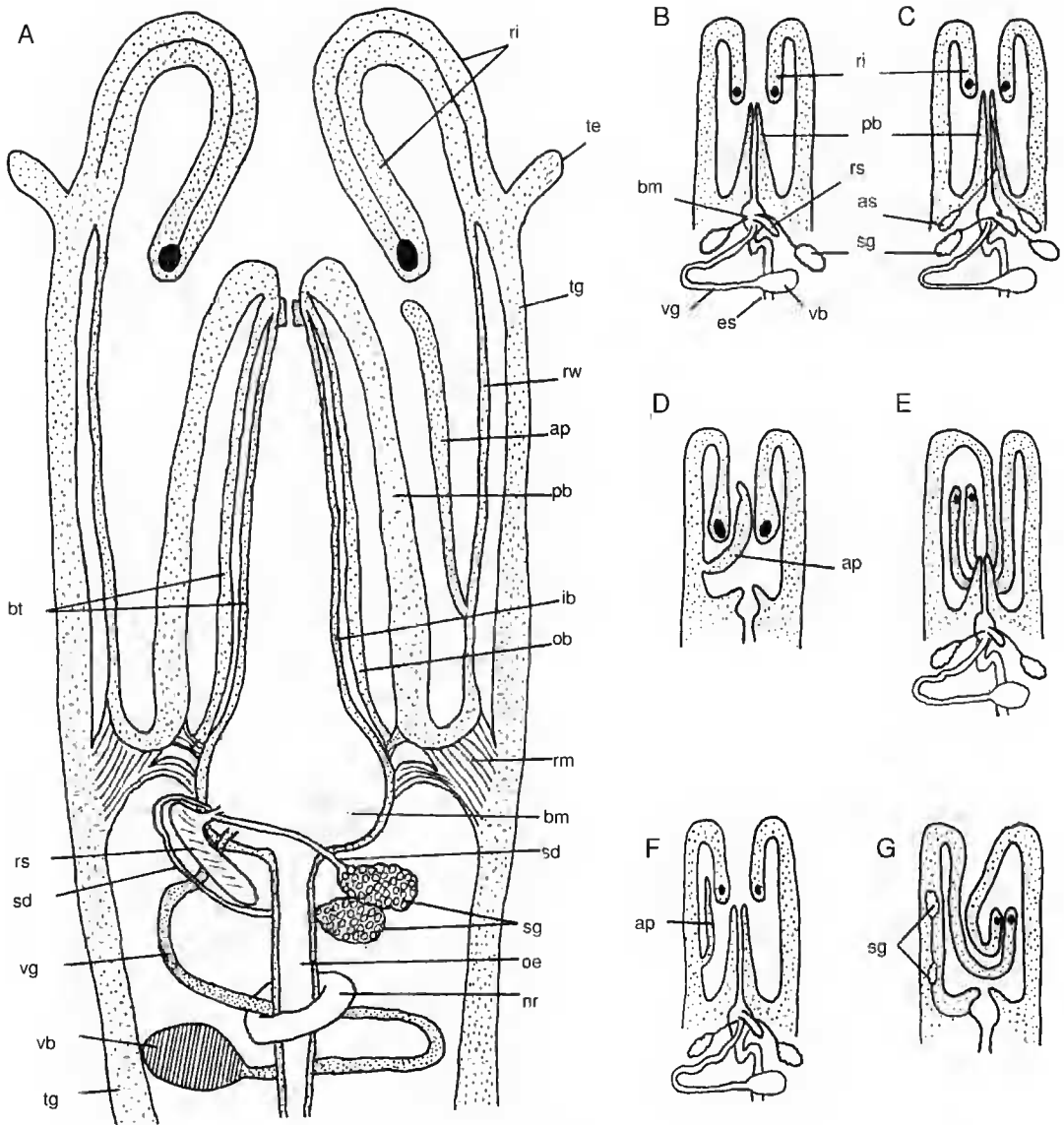


FIG. 7. — Schematic pictures: **A**, composite-synoptic diagram of the terebrid foregut based on species studied herein, ventral view, not to scale or proportion; **B-G**, diagram of foregut in dorsal view of studied species following the model in the current literature, not to scale or proportion: **B**, *Hastula cinerea*; **C**, *H. hastata*, *Terebra taurina*; **D**, *T. brasiliensis*; **E**, *T. spirosculata*; **F**, *T. crassireticula*; **G**, *T. leptapsis*; **G**, *T. gemmulata*.

retractor muscle pair (rm), and in inner surface of haemocoel. Posterior extremity of inner buccal tube wall fused directly to buccal mass. Pair of retract-or muscles (rm) also inserts in buccal mass lateral surface (Fig. 5C). Radular sac long, curved, with several radular teeth, opening sub-

terminally in mid-ventral region of buccal mass (Fig. 5E). Radula composed of about twenty single, hollow, marginal teeth; each tooth conical, base barbed, tip narrowing gradually, circular in section (but not altogether fused); length about 650 μ m. Tip sharply pointed, with a

small, narrow orifice (Fig. 6A, B). Salivary glands form pair of hemi-spheres of glandular, white tissue connected to each other; their ducts contour oesophagus and insert at anterior and posterior side of base of radular sac aperture (Fig. 5C, E); gray, iridescent. Venom gland very long and convolute, about half anterior to and half posterior to nerve ring, no apparent change in its inner tissue along its length; inserts in buccal mass close to and at left of radular sac aperture. Muscular bulb rather long, conical, with broad distal region (Fig. 5A, B); wall composed of two layers of muscular tissue, inner layer slightly thinner than outer layer. A sketch of foregut structures shown in Figure 7B. Inner surface of buccal mass with several longitudinal, low, subequal folds (Fig. 5E), some of them converge to aperture of venom gland and of radular sac; these folds become discontinuous at anterior end of oesophagus, marked by a sudden interruption of folds and a reduction of their number (Fig. 5E). Oesophagus a long, narrow tube with several longitudinal folds similar to those of buccal mass (Fig. 5E), folds tall in some specimens (Fig. 8B); no interior glands present. Stomach simple, curved (Fig. 5F), located half a whorl posterior to kidney and immersed in digestive gland. Duct to digestive gland single, located in mid-ventral region of stomach; after a short distance bifurcates into anterior and posterior branches. Digestive gland with about 5.5 whorls posterior to stomach and half a whorl anterior to it, close to pericardium level (Fig. 2B), pressed between kidney and oesophagus, beige. Intestine narrow, with thin walls and an almost smooth inner surface; runs to left of and ventral to margin of kidney. Rectum and anus described above. Other details in Marcus & Marcus (1960: 37-44).

Genital system (Figs 2A; 4A, B)

Male. Prostate thick-walled, of about same length as rectum, running ventrally to it, attached to pallial floor, with a small longitudinal aperture in its posterior ventral region. Vas deferens, after prostate, runs along floor of right margin of pallial cavity. Penis moderately long (Fig. 2A), cylindrical; penis duct slightly convoluted, near left margin of penis. Distal end of penis with a concavity turned to right, in its centre a rather

large papilla where penis duct opens (Fig. 4B). Penis papilla close to right margin. Other details in Marcus & Marcus (1960: 44-45, figs 14, 15).

Female. Pallial gonoduct with a well-developed terminal pouch (Fig. 4A), with a longitudinal furrow turned to right close to columella, occupying about half total length of pallial gonoduct. Other details in Marcus & Marcus (1960: 45-47, figs 16-18).

Nervous system

As described by Marcus & Marcus (1960: 34-37, fig. 5).

Hastula hastata (Gmelin, 1791)

(Figs 1C, D; 3B, C; 6D, E; 7C; 8A; 9-11)

Synonymy: cf. Matthews *et al.* (1975: 101) and Bratcher & Cernohorsky (1987: 184).

Others: *Hastula hastata* – Rios 1985: 131 (fig. 591). – Calvo 1987: 171 (fig. 161). – Rios 1994: 181 (fig. 842).

MATERIAL EXAMINED. — **Bahia.** Brazil, Salvador, Itapuã Beach, 27.II.1997, Simone coll., 2 specimens observed alive (MZSP 28426).

Rio de Janeiro. Brazil, Búzios, Ferradura Beach, 17.I.1994, Simone coll., 30 specimens (MZSP 28713). — Ilha Grande Bay, RV *Emilia*, stn 288, 24 m, 30.VII.1966, 1 ♀ (MZSP 24671). — RV *Emilia*, stn 269, 30.2 m, 19.VII.1966, 1 ♀ (MZSP 24669).

MEASUREMENTS. — MZSP 24671: 32.1 × 8.1 mm.

DISTRIBUTION. — From Florida, USA, to Santa Catarina, Brazil.

HABITAT. — Infratidal, crawling on sand or sandy mud.

DESCRIPTION

Shell (Fig. 1C, D)

A description of the shell can be found in Matthews *et al.* 1975: 101 (figs 35-37); Bratcher & Cernohorsky, 1987: 184 (fig. 222a, b). The shell bears two spiral colour bands on each whorl, pale brown and beige, some specimens entirely beige. Periostracum thin, opaque, black. Outline rather short and cylindrical, last few whorls being of about the same diameter. Sculpture of well-developed axial ridges.

Head-foot (Fig. 9A, D)

Colour homogeneous cream. Head little differentiated from head-foot axis (Fig. 9A). Tentacles short, pointed, directed laterally (Fig. 9D). Eyes small, dark, located at tentacle bases (Fig. 9D). Basal, proximal introvert aperture rather broad, transverse, anterior and ventral to tentacles. Foot large, occupying more than half a whorl, with a shallow furrow between mesopodium and epipodium (Fig. 9A); sole with folded borders. Columellar muscle occupying about two whorls, rather thin. Males with penis in central-right region posterior to head.

Operculum (Fig. 3B, C)

Large, unguiculate, pale brown, nucleus terminal (Figs 3B, C). Occupying entire shell aperture. Inner surface with a large oblique scar near inner and posterior margins (Fig. 3C).

Mantle organs (Figs 9B, C; 10)

Mantle border simple, not pigmented. Siphon well-developed, long, pale cream, with smooth borders; both sides of siphon base with well-developed siphon appendices, standing out from remainder of border (Fig. 9B: sp), sometimes both extend through shell aperture. Mantle cavity occupying about two whorls. Osphradium elliptical, about one third of gill length; with several uniform filaments on both sides of osphradial ganglion; right filaments similar in size to left filaments; each filament scalloped by about three digitations (Fig. 9C). Gill long and narrow, extending about nine tenths of pallial cavity length; anterior extremity close to mantle border, with only a short portion of ctenidial vein present, in form of a very small septum (Fig. 9B: ac); filaments begin gradually a short distance from anterior extremity; each filament triangular, apex located at right, right margin almost straight; gill posterior extremity very close to pericardium. Ctenidial vein uniformly narrow, except for a broader anterior extremity. A proportionally broad space between gill and rectum. Hypobranchial gland thin, located in posterior two thirds of cavity, at left of rectum, pale cream. Anal gland with some slender, irregular acina immersed in right margin of hypobranchial gland in anterior half of rectum, distant from

anus (Figs 9B; 10), purple. Pallial gonoducts run along right margin of posterior two thirds of pallial cavity, attached also to pallial floor. Rectum narrow, lying dorsally to prostate in males, ventrally and to left region of pallial oviducts in females; in females, before anus, rectum crosses to dorsum and remains attached to mantle. Anus close to anterior extremity of pallial oviduct in females (Fig. 10) or prostate in males (Fig. 9B); bearing a small, ventral papilla at its border. Anterior third of pallial right margin without inner structures.

Circulatory and excretory systems (Fig. 9F)

Heart of medium size, similar to that of preceding species. Kidney of almost one quarter whorl, flattened, located in right region of posterior limit of pallial cavity. Kidney apparently without large inner chambers and free from rectum; internally with only a flattened chamber and a large, massive glandular mass, triangular in section, pale cream. Nephridial gland small, pale cream, section triangular, bordering dorsal margin of membrane between kidney and pericardial chambers. Nephrostome a transverse slit in middle region of membrane between kidney and pallial cavity.

Digestive system

(Figs 6D, E; 7C; 8A; 9A, E, F; 11B)

Organization rather similar to that of preceding species. Rhynchodeal introvert occupying about half of remainder of foregut length, cylindrical (Figs 9A; 11B); walls with thick muscles, double. Rhynchodeal introvert distal aperture (rhynchostome) large; with a thin sphincter. Inner rhynchodeal wall very thin, transparent, covering inner surface of anterior half of haemocoel as in preceding species (Fig. 11B). Proboscis conical, of about same length as rhynchodeal, connected at its base to rhynchodeal wall and retractor muscles; proboscis distal region very narrow and long, generally preserved part protracted; a muscular thickening grips a tooth close to proboscis tip. Buccal mass cylindrical and elongated, with a long, broad buccal tube that also becomes very narrow distally like proboscis. Buccal tube with outer muscular wall, consisting mainly of longitudinal muscle fibres; inner wall thin, with seve-

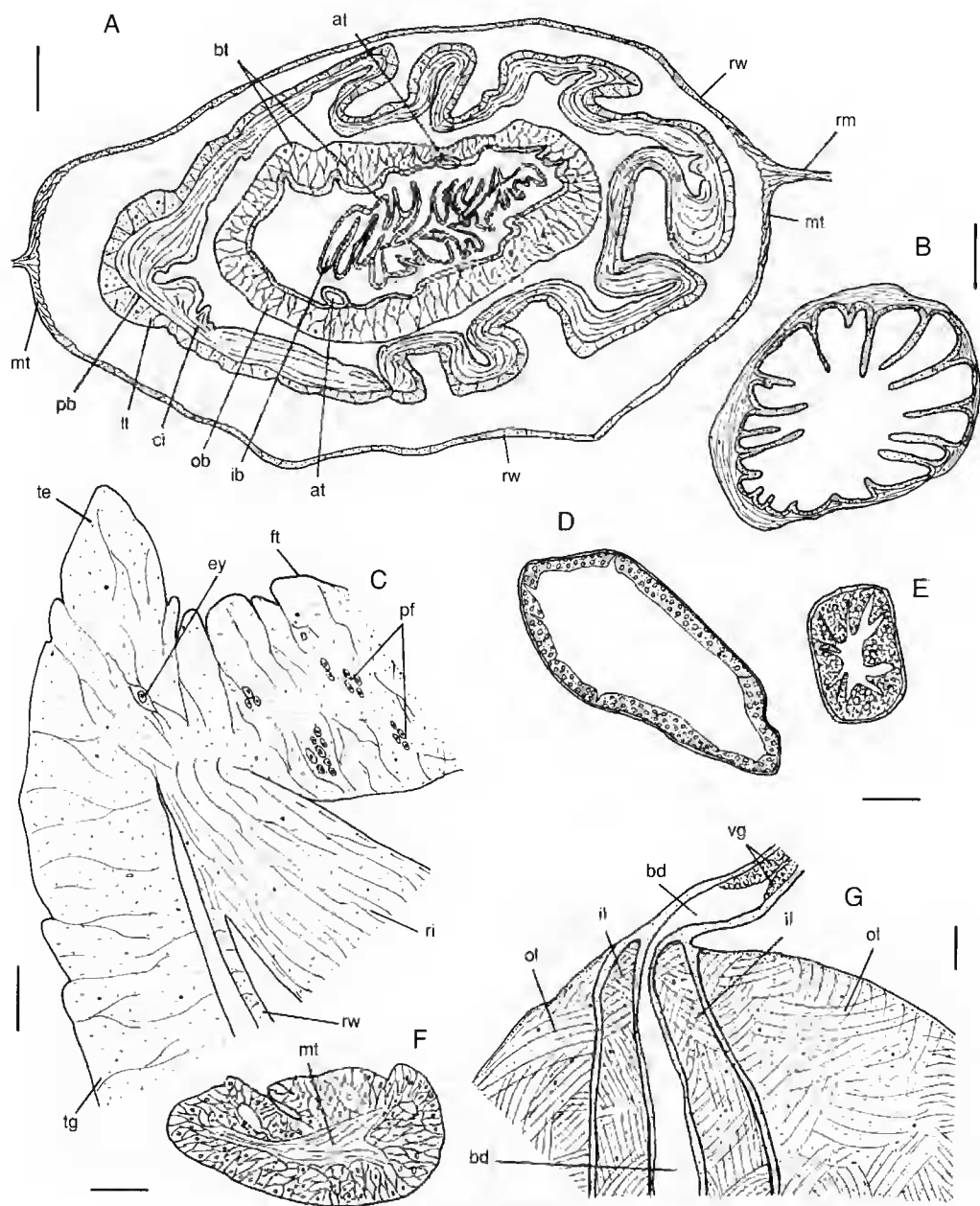


Fig. 8. — Interesting aspects of serial sections, semi-diagrammatic representations; A, *Hastula hastata*, transverse section at the basal level of the proboscis, head tegument removed; B, *H. cinerea* transverse section of anterior region of oesophagus showing internal folds; C, *Terebra gemmulata*, antero-posterior section in middle region of right tentacle, just at the level of the eye, anterior-dorsal extremity of foregut also shown; D, E, *T. spirasulcata*, transverse sections of venom gland, D, proximal (anterior to nerve ring), E, distal region; F, *T. brasiliensis*, accessory proboscis structure, transverse section of middle region; G, *T. taurina*, proximal (anterior) extremity of venom bulb and distal extremity of venom gland sectioned just at their duct level. Thickness of section: 7 μ m, Mallory stain. Scale bars: 100 μ m.

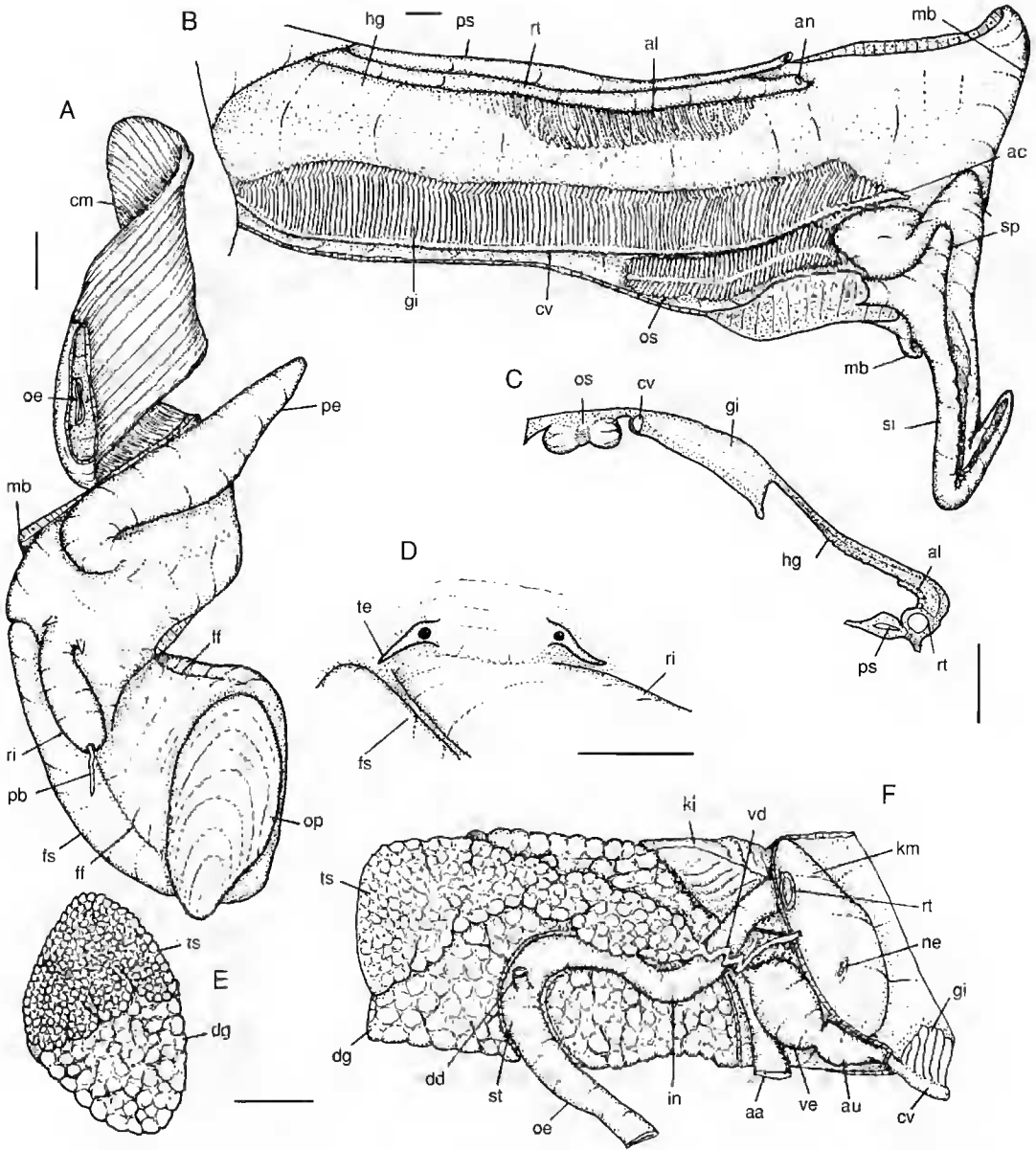


FIG. 9. — *Hastula hastata*, anatomy; A, ♂ head-foot, mantle removed, introvert protracted; B, mantle organs, ventral-internal view; C, transverse section of middle region of pallial roof; D, detail of A in region of tentacles; E, transverse section of visceral mass half a whorl posterior to the stomach; F, visceral mass anterior region, ventral view, digestive gland near stomach partially removed, kidney and pericardium opened. Scale bars: A, 1 mm, B-F, 0.5 mm.

ral longitudinal, internal, tall folds (Fig. 8A). Anterior extremity of buccal tube smooth internally. A pair of retractor muscles (rm) is also inserted in lateral surface of buccal mass. Two acces-

sory salivary glands, one on each side of proboscis base, close to insertion of retractor muscles (Fig. 11B: as); each gland elliptical, long, occupying about one quarter of length of rhynchodeal

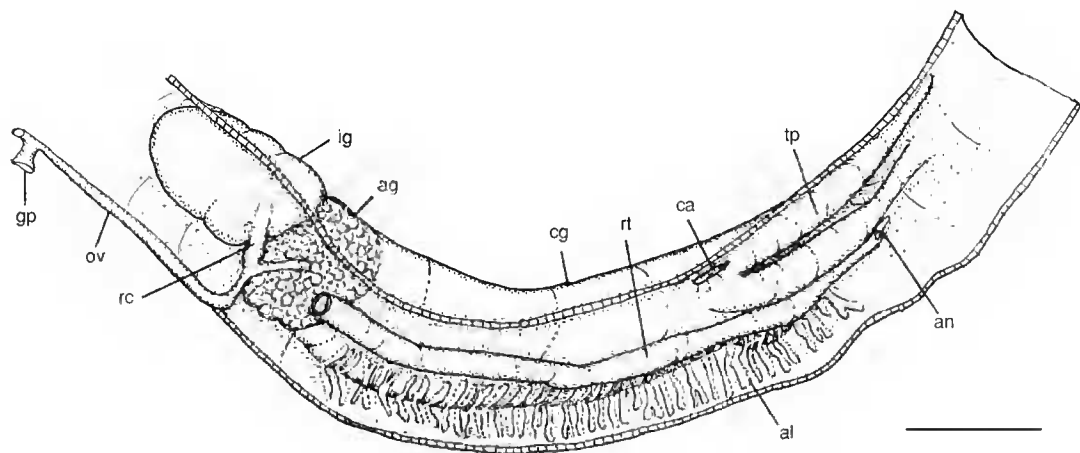


FIG. 10. — *Hastula hastata* pallial oviduct, ventral view, part of its adjacent regions of mantle and visceral mass also shown. Scale bars: 1 mm.

cavity length; their ducts run in outer wall of buccal tube (Fig. 8A), fusing with each other in middle level of proboscis. Radular sac very small, elongated, curved, with about twenty radular teeth, opening sub-terminally in ventral-mid region of buccal mass (Fig. 11B). Radula with very small teeth, about 120 μm in length; each tooth with two distinct regions (Fig. 6D, E): basal region broader than distal one, hollow, base barbed, circular in section (but not altogether fused); distal region about same length as basal one, narrow, almost solid except for a longitudinal aperture in its proximal region, tip sharply pointed. Salivary glands similar to those of preceding species. Venom gland very long, narrow and convolute (Fig. 11B), about half anterior and half posterior to nerve ring; without apparent change of inner tissue along its length; inserted in buccal mass close and at left of radular sac aperture. Muscular bulb elliptical, short, almost circular in section; with two muscular layers, inner layer about half thickness of outer layer. Inner surface of buccal mass similar to that of preceding species. A sketch of foregut structures is shown in Figure 7C, E.

Oesophagus a long, narrow tube, anterior region flattened and with smooth inner surface, posterior region narrow with several longitudinal folds; no interior glands. Stomach simple, curved,

located half a whorl posterior to kidney, immersed in digestive gland, almost restricted to left half of this region (Fig. 9F). Duct to digestive gland single, located in mid-ventral region of stomach. Digestive gland (Fig. 9E, F) occupying about 5.5 whorls posterior to stomach and half a whorl anterior to it, beige. Intestine narrow, with thin walls, inner surface almost smooth, sigmoid; runs left and ventral to kidney (Fig. 9F).

Genital system (Figs 9A, E, F; 11A, C, D)

Male. Testis (Figs 9E; 11A) rather short, located in peri-columellar region of second whorl posterior to stomach, gradually narrowing and becoming a thick walled duct which also runs close to columella (Fig. 9F), opening to pallial cavity near and ventral to rectum. Prostate thick-walled, rather narrow and long, close about half length of rectum, without detectable aperture. Vas deferens runs along floor of right margin of pallial cavity; in its anterior region it is immersed in head tegument and emerges into haemocoel a short distance before its entrance to penis (Fig. 11D); in this area vas deferens thicker. Inner region of penis base strongly muscular (Fig. 11D), a flattened muscle crosses through foregut and inserts in ventral surface of haemocoel. Sometimes these penis muscles dislocate foregut structures to left. Penis rather short

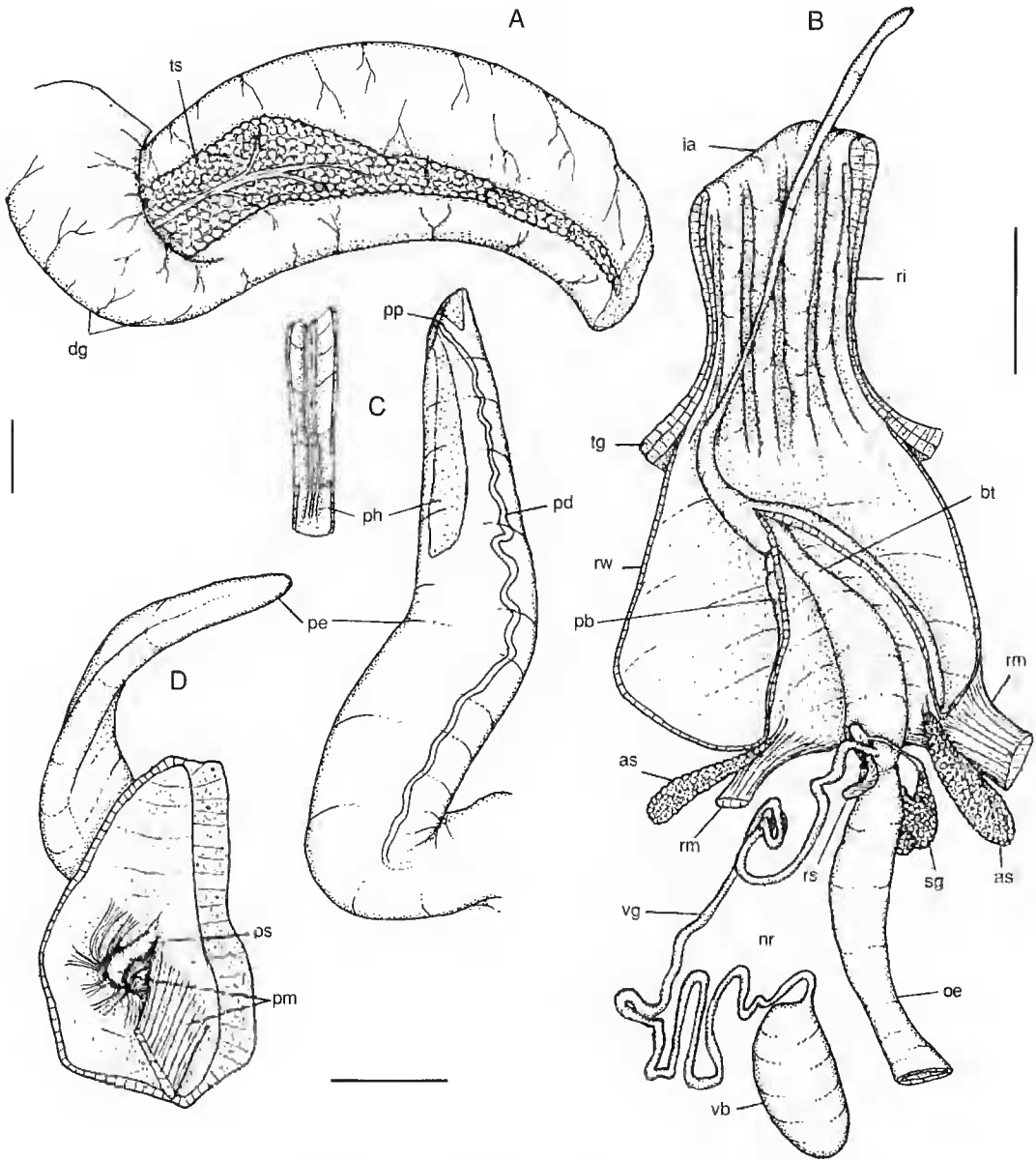


FIG. 11. — *Hastula hastata*, anatomy; **A**, visceral mass posterior to stomach, partially uncoiled, ventral view; **B**, foregut, ventral view, rhynchodeal wall and introvert opened longitudinally, proboscis partially opened longitudinally, nerve ring removed (its position indicated); **C**, penis, dorsal view, with a detail of interior surface of the right wall of its chamber; **D**, internal surface of dorsal wall of haemocoel, just in region of penis, showing penis duct and muscles. Scale bars: 1 mm.

(Fig. 9A) – about half length of pallial cavity, flattened; basal half broader than distal half, which tapers gradually; penis duct very narrow, slightly convoluted near left margin of penis

(Fig. 11C). Distal end of penis with a concavity strongly turned to right, with a rather large papilla in its centre through which penis duct opens (Fig. 11C). Right region of this concavity

very deep – about one third of penis length, producing a long chamber with right margin bearing a pair of low longitudinal folds (Fig. 11C: ph). Penis papilla closer to right margin of penis than to left.

Female. (Fig. 10) Ovary similar in position to testis. Visceral oviduct very narrow, running close to columella, with a small gono-pericardial aperture; inserted in pallial gonoduct anterior to ingesting gland. Ingesting gland hemispherical, orange, with a short receptaculum seminis connecting it to oviduct. Albumen gland short, anterior to ingesting gland. Capsule gland long – about half of total pallial oviduct length, cylindrical, with a central, flattened duct which opens as a small slit at right of terminal pouch base. Terminal pouch elliptical, with a longitudinal furrow turned to right close to columella and opening anteriorly; occupying about one third of total length of pallial gonoduct.

Genus *Terebra* Bruguière, 1789

Terebra brasiliensis Smith, 1873

(Figs 3G; 7D; 8F; 12E; 13B; 14E; 15; 16)

Synonymy: cf. Matthews *et al.* (1975: 91) and Bratcher & Cernohorsky (1987: 160). Others: *Terebra brasiliensis* – Rios 1985: 130 (fig. 583). – 1994: 179 (fig. 832).

MATERIAL EXAMINED. — Rio de Janeiro, Brazil, RV W. Benard, stn 1475, 23°08'S, 43°46'W, off Rio de Janeiro, 40 m, 8.III.1971: 1 ♂, 1 ♀, 3 shells (MZSP 19403).

MEASUREMENTS. — In millimeters MZSP 19403: ♀ 11.0 × 3.3; ♂ 9.0 × 2.8.

DISTRIBUTION. — Rio de Janeiro, Brazil.

HABITAT. — From 20 to 40 m deep. Sandy substrates.

DESCRIPTION

Shell (Figs 12E; 13B; 14E)

Shell description found in Matthews *et al.*, 1975: 91–92 (figs 9–13); Bratcher & Cernohorsky, 1987: 160 (figs 186a, b). Sculpture lacking except for axial subsutural ribs, giving an almost smooth surface (Figs 12E; 13B). In comparison with other terebrids, *T. brasiliensis* has few teleo-

conch whorls and a proportionally large protoconch (Fig. 14E), giving an appearance of immaturity, but all specimens are rather similar and have genital glands developed.

Head-foot (Figs 15B, C; 16A)

Colour homogeneous yellowish cream. Head weakly differentiated from head-foot axis (Fig. 15B). Tentacles very short, dorso-ventrally flattened, tip rounded (Figs 15B, C; 16A). Eyes small, dark, located in middle of tentacles. Basal, proximal introvert aperture rather broad, transverse, located anteriorly and ventrally to tentacles. Foot occupying almost half whorl; sole with folded borders; a shallow furrow separates mesopodium from metapodium; furrow of pedal glands anterior (Fig. 15B). Columellar muscle of about two whorls, rather thick. Males with penis of medium size, originating in central-right region posterior to head.

Operculum (Figs 3G; 15B)

Large, unguiculate, pale brown, nucleus terminal (Fig. 3G). Occupying entire shell aperture (Fig. 15B).

Mantle organs (Figs 15A, D, F; 16D)

Mantle border simple, not pigmented. Siphon well-developed, yellowish cream, with smooth borders. Mantle cavity of about two whorls (Fig. 15A). Osphradium elliptical, long, about two thirds of gill length; with several, uniform filaments; right filaments larger than left, angular, more numerous than left filaments (Fig. 15D); a short portion of anterior left region of osphradium with filaments lacking (Fig. 15A). Gill narrow and long, about two thirds of pallial cavity length; anterior end rather far from mantle border, with only a short portion of ctenidial vein present, in form of a very small septum (Fig. 15A: ac); filaments begin gradually at some distance from anterior end; each filament triangular, low, apex about central, margins almost straight; gill posterior end far from pericardium. Ctenidial vein narrow and uniform all along its length, except for its broader anterior extremity; a long posterior region free from filaments (Fig. 15A, F). A proportionally narrow space between gill and rectum. Hypobranchial gland thin,

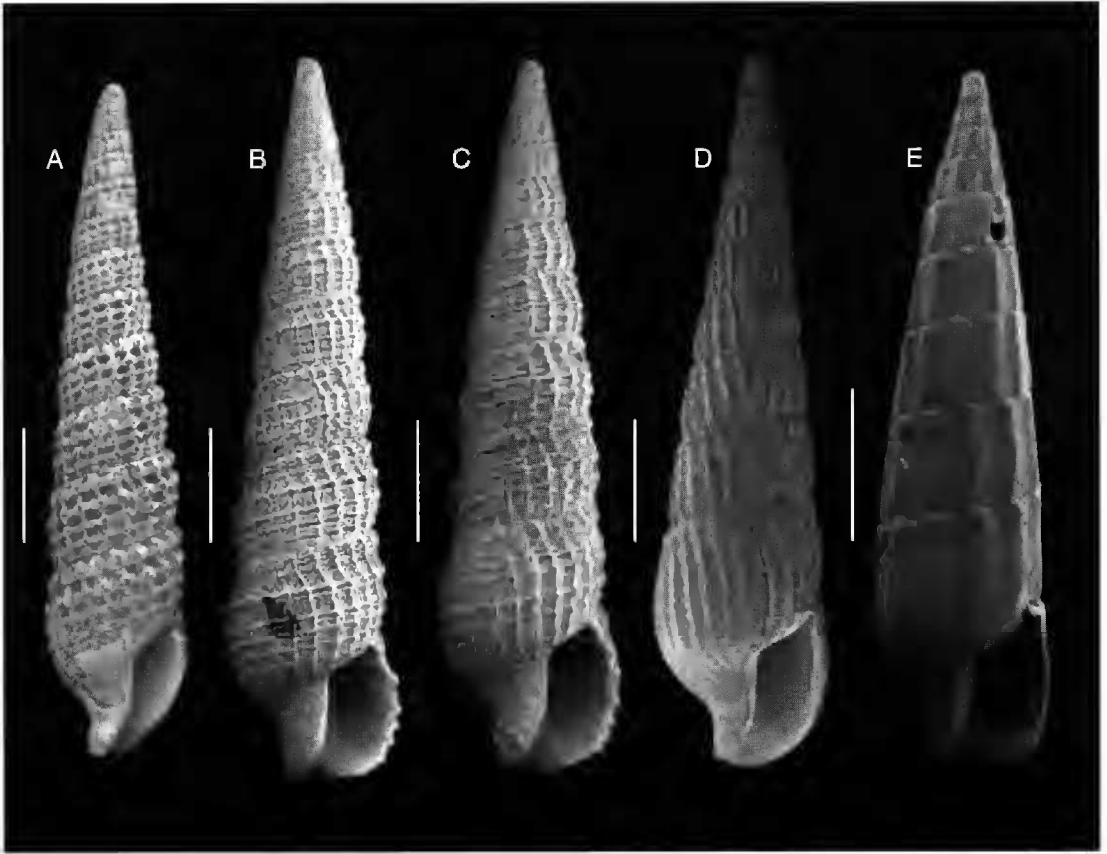


FIG. 12. — Shells in frontal view, SEM (only in E the shell is coated with gold); A, *Terebra crassireticula* n. nom., MNHN; B, *Terebra leptapsis* n. sp., holotype; C, same species, paratype; D, *Terebra sterigma* n. sp., holotype; E, *Terebra brasiliensis*. Scale bars: 2 mm.

located in posterior half of cavity, at left of rectum, pale cream. Anal gland not differentiable. Pallial gonoducts run along right margin of posterior half of pallial cavity. Rectum narrow, lying ventral and to left of pallial gonoducts, afterwards attached to mantle (Figs 15A; 16D). Anus in front of anterior extremity of pallial oviduct in females or prostate in males; bears no papilla. Anterior half of pallial right margin without internal structures.

Circulatory and excretory systems (Fig. 15E, F)

Heart of medium size, position similar to that of preceding species. Kidney of almost one quarter whorl, flattened, located at right of posterior limit of pallial cavity; without inner chambers, consisting of a mass of whitish tissue with trans-

verse furrows; furrows more evident in posterior region where rectum borders. Nephridial gland small, pale cream, triangular in section, bordering dorsal margin of membrane between kidney and pericardial chambers. Nephrostome a transverse slit in middle region of membrane between kidney and pallial cavity.

Digestive system (Figs 7D; 8F; 15E; 16A-C)

Rhynchodeal introvert large, conical, cylindrical length almost equal to rhynchocoel length, muscular walls thick (Fig. 16A, B). Outer region (in retracted condition) mainly of longitudinal fibres and inner region mainly of circular fibres; both muscular layers closely connected to each other by connective tissue, without any space between. Distal aperture of rhynchodeal introvert (rhyn-

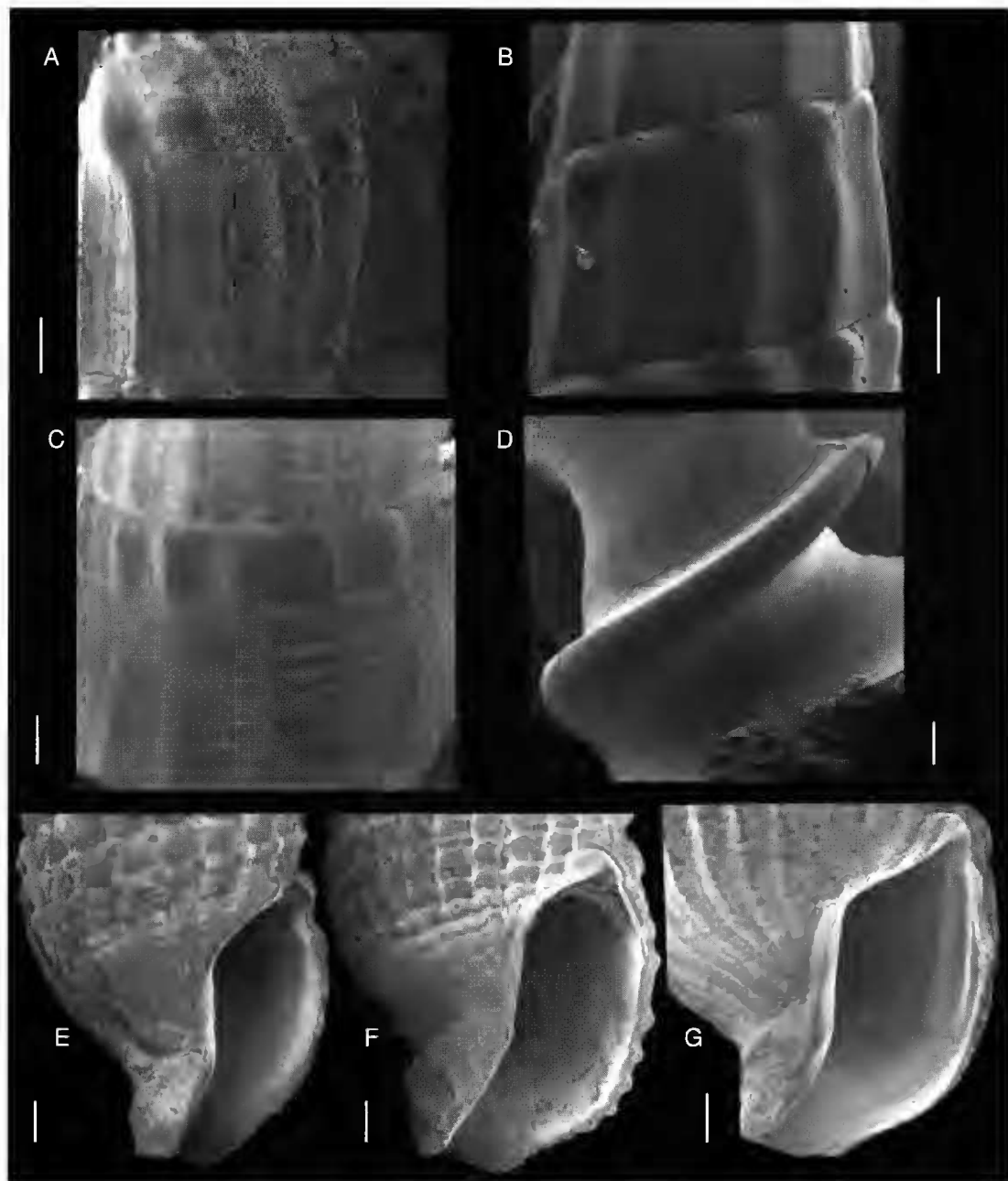


FIG. 13. — Details of shells in SEM; **A**, detail of shell sculpture at the level of the penultimate whorl of *T. gemmulata*; **B**, same of *T. brasiliensis*; **C**, same of *T. spirosulcata*; **D**, *T. taurina*, columella of penultimate whorl exposed; **E**, detail of aperture of *T. crassireticula*; **F**, same of *T. leptapsis*; **G**, same of *T. sterigma*. Scale bars: 0.5 mm.

chostome) very large and with a lateral expansion on each side (Fig. 16B); a very large sphincter present. Inner rhynchodeal wall very thin, trans-

parent, covering inner surface of anterior half of haemocoel as in preceding species (Fig. 16A-C). Accessory proboscis structure large – about same

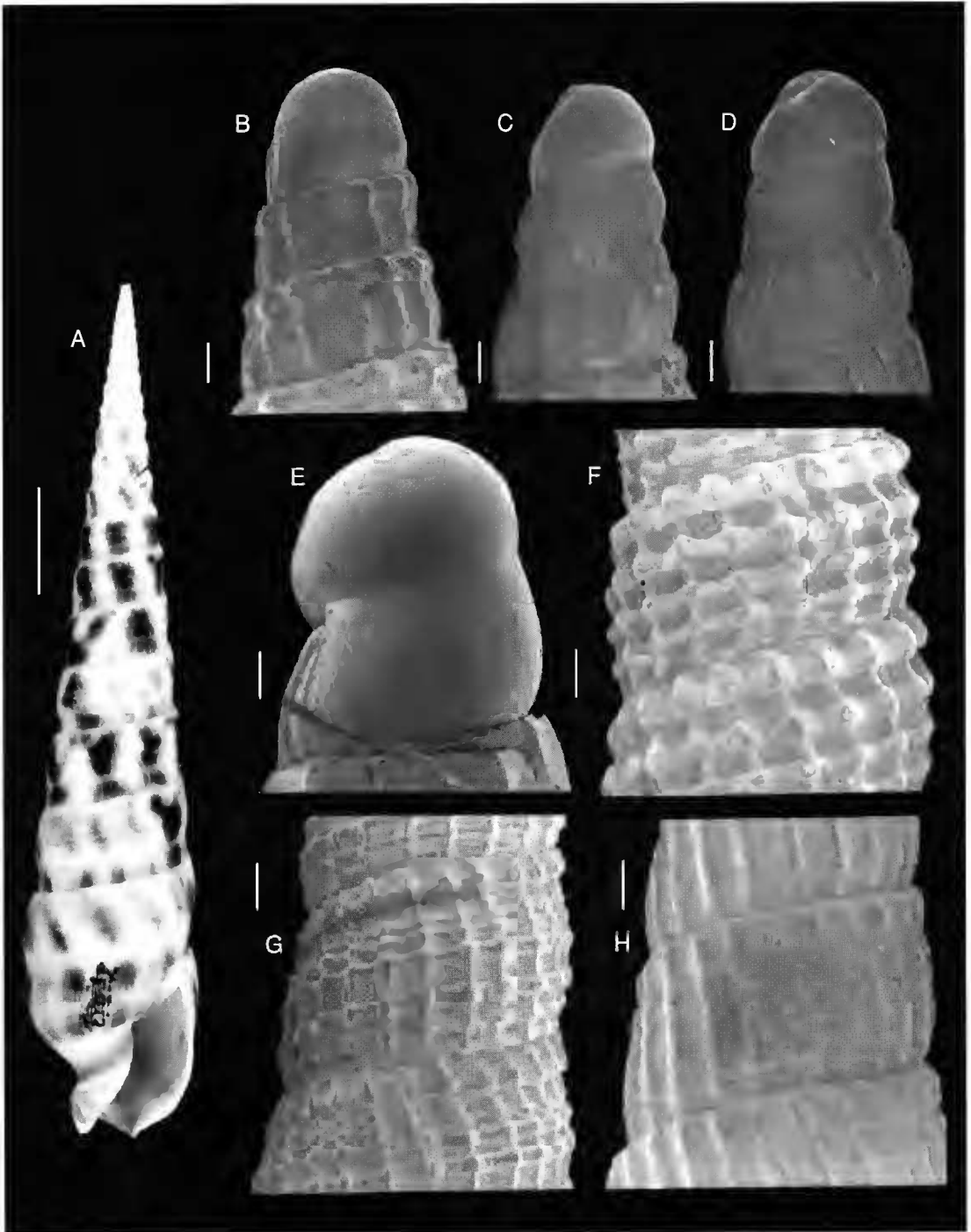


FIG. 14. — Shells (B-H in SEM); A, *Terebra taurina*; B, detail of protoconch of *T. crassireticula*; C, same of *T. leptapsis*; D, same of *T. sterigma*; E, same of *T. brasiliensis*; F, detail of shell sculpture at the level of the penultimate whorl of *T. crassireticula*; G, same of *T. leptapsis*; H, same of *T. sterigma*. Scale bars: A, 10 mm; B-D, 0.2 mm; E, 0.1 mm; F-H, 0.5 mm.

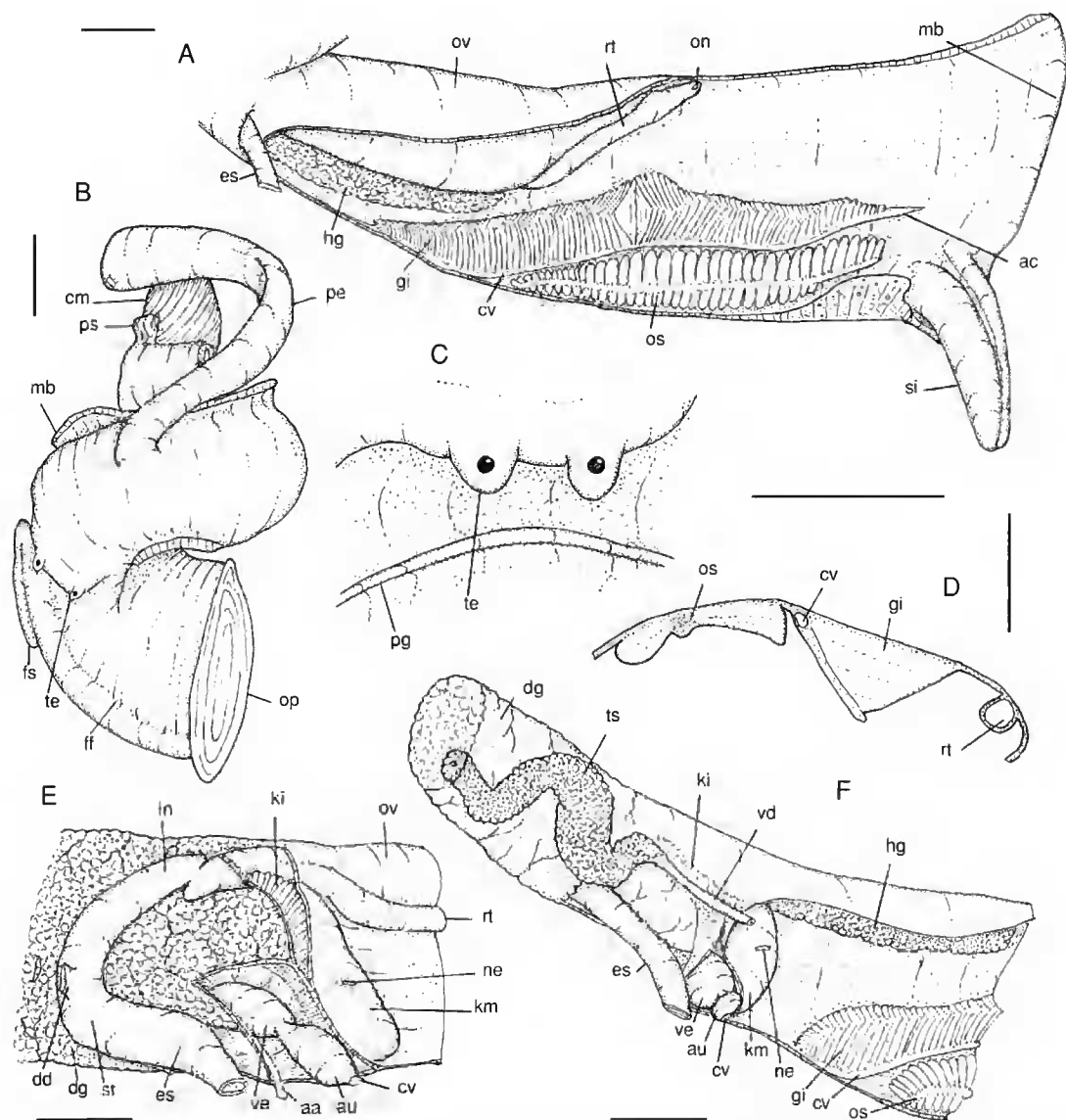


FIG. 15. — *Terebra brasiliensis*, anatomy; **A**, pallial organs, ventral-internal view; **B**, head-foot of male, mantle removed; **C**, same, detail of tentacle region; **D**, pallial cavity roof, transverse section of its middle region; **E**, anterior region of visceral mass and adjacent pallial cavity, ventral view, part of digestive gland adjacent to stomach removed, pericardium and kidney partially opened; **F**, whorls adjacent to posterior limit of pallial cavity, ventral view. Scale bars: 0.5 mm.

length as rhynchiocoel, flattened, originating in middle-left region of rhynchodeal wall inner surface, in proximal region very thin, gradually becoming thick and broader (Fig. 16B, C), tapering suddenly at tip. Central region of accessory proboscis structure muscular and peripheral

region glandular (Fig. 8F). Proboscis very small, reduced, present only as muscular ring around buccal mass (Fig. 16B, C). Buccal mass spherical. Pair of retractor muscles reduced. Radular sac and salivary glands not present. Venom gland and muscular bulb also absent. A sketch of fore-

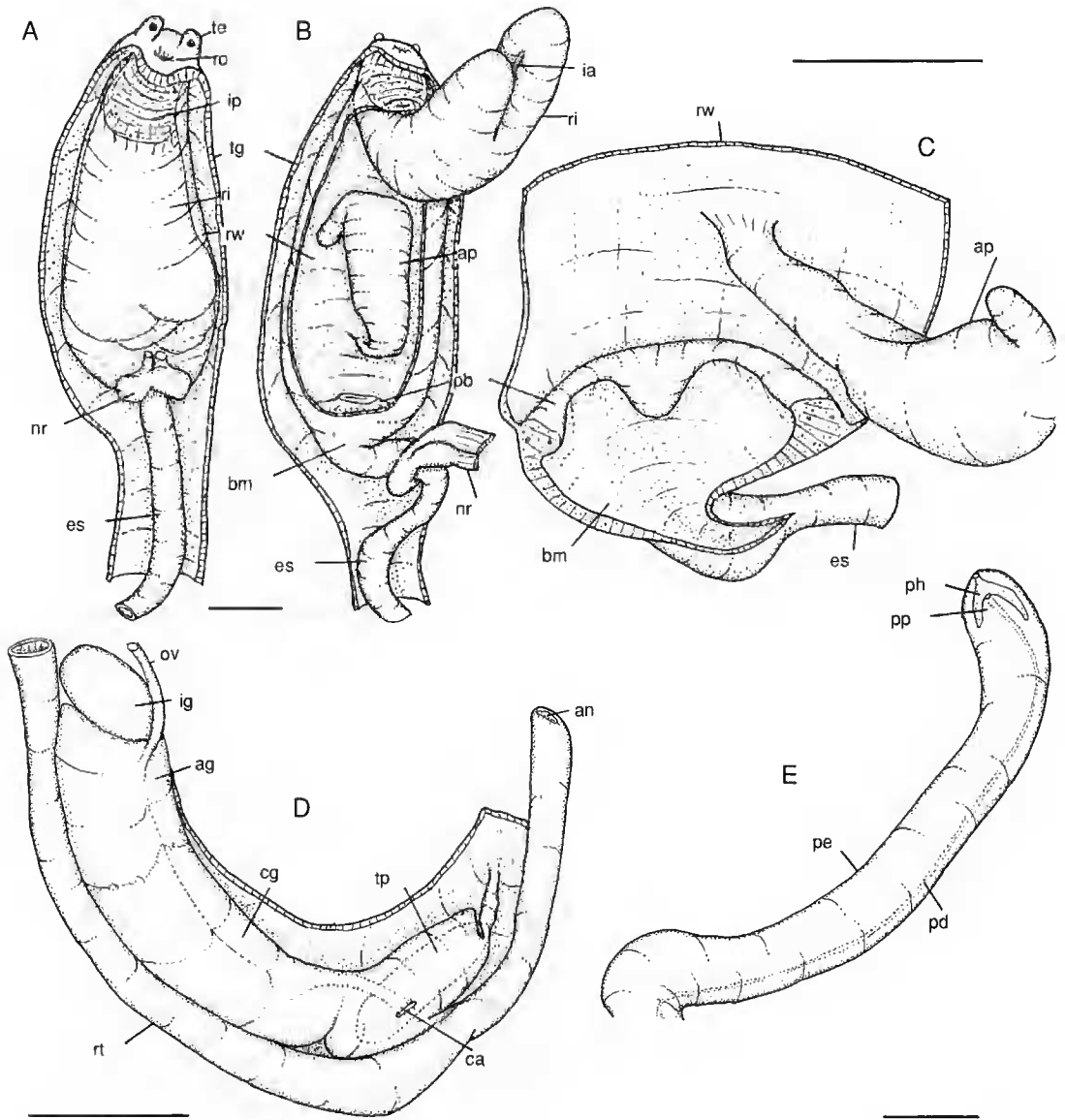


FIG. 16. — *Terebra brasiliensis*, anatomy; **A**, head and haemocoel, ventral view, foot and columellar muscle removed; **B**, same, with ventral region of rhynchodeal wall removed, introvert and nerve ring reflected to show dorsal surface; **C**, posterior extremity of rhynchodeal wall and buccal mass both opened longitudinally, internal surface exposed; **D**, pallial oviduct and adjacent rectum, ventral view; **E**, penis, dorsal view. Scale bars: 0.5 mm.

gut structures shown in Figure 7D. Inner surface of buccal mass and oesophagus smooth (Fig. 16C). Oesophagus long and narrow. Stomach simple, curved, located half whorl posterior to kidney (Fig. 15E), immersed in diges-

tive gland. Duct to digestive gland single, located in middle, ventral region of stomach. Digestive gland of about 3.5 whorls posterior to stomach and also half a whorl anterior to it, beige. Intestine broad, slightly sinuous, with thin walls,

inner surface almost smooth; runs along left and ventral margins of kidney (Fig. 15E). Rectum and anus described above.

Genital system (Figs 15B, F; 16D, E)

Male. Testis similar to that of preceding species. Visceral vas deferens runs close to columella; about one whorl before kidney becoming very broad, with thick, iridescent walls and rather coiled; narrowing at level of kidney (Fig. 15F), exiting to pallial cavity in middle region of posterior limit of cavity, running along floor of pallial cavity within tegument (Fig. 15B). Prostate not differentiable. Penis about half of pallial cavity length, flattened (Fig. 15B); rather uniform in width; penis duct very narrow, nearly straight, near left margin of penis (Fig. 16E). Penis distal end with a deep concavity turned to right and with a small aperture; in its centre a rather large papilla where penis duct opens.

Female. Ovary similar in position to testis. Visceral oviduct very narrow, running close to columella, inserted in pallial oviduct at right posterior extremity of albumen gland (Fig. 16D). Ingesting gland rather spherical, posterior to albumen gland, with a very short receptaculum seminis connected directly with pallial oviduct in left margin. Albumen gland short, thick-walled, white; limit between it and capsule gland imprecise. Capsule gland yellow, about half of total pallial oviduct length, cylindrical, with a central, flattened duct (Fig. 16D); this duct narrows abruptly in right posterior extremity of capsule gland, crossing right posterior region of terminal pouch, bearing several narrow longitudinal folds, opening as a small pore located in about mid-ventral region of terminal pouch. Terminal pouch broad, cylindrical, with a small terminal anterior aperture, close to columella; terminal pouch comprises a deep, blind sac (Fig. 16D); left lip of aperture with a long fold which gradually disappears; total length of terminal pouch about half that of pallial oviduct.

***Terebra crassireticula* n. nom.**

(Figs 3F; 6C; 7F; 12A; 13E; 14B, F; 17)

Terebra reticulata Simone & Verissimo, 1995: 460-466, figs 1-8 (pre-occupied name) (*non* Sowerby 1840).

TYPE MATERIAL. — **SE Brazil.** RV *Marion-Dufresne*, stn DC75, 18°59'S, 37°50'W, 295 m, V.1987, 1 shell MNHN. — Stn CB92, 19°34'S, 38°55'W, 340-360 m, V.1987, 160 shells MNHN. — Stn CB96, 21°32'S, 40°09'W, 295 m, V.1987, 46 shells MNHN. — Stn CB98, 21°35'S, 40°31'W, 900 m, V.1987, 1 eroded shell MNHN. — Stn CB103, 23°36'S, 42°02'W, 200-217 m, V.1987, 1 shell MNHN. — Stn CB104, 23°42'S, 42°07'W, 430-450 m, V.1987, 1 shell MNHN. **São Paulo, Brazil,** off Ilha Bela, RV *W. Besnard*, 23°57.5'S, 44°53'W, 75 m, 27.VII.1986, 2 specimens (MZSP 28393).

DISTRIBUTION. — From Rio de Janeiro to São Paulo, Brazil.

HABITAT. — Deep waters, from 75 to 900 m depth (commonest between 200 and 450 m depth), sandy substrates.

MEASUREMENTS. — In millimeters, followed by number of axial and spiral ribs in penultimate whorl. MNHN stn CB96: 15.5 × 3.9, 19, 3; 17.4 × 3.7, 19, 4.

REMARKS

Males and mature females were not examined in the original description. With additional fixed material provided from a new collection and a loan from MNHN the following complementary morphological description is possible.

COMPLEMENTARY DESCRIPTION

Shell (Figs 12A; 13E; 14B, F)

Shell description can be found in Simone & Verissimo (1995: 462-463, figs 1-3).

Head-foot and operculum (Figs 3F; 17A, C)

As described by Simone & Verissimo (1995: 463, figs 4-5).

Mantle organs (Fig. 17B, E, F)

Description found in Simone & Verissimo (1995: 464, fig. 6) particularly accurate, following data additional: anus located near middle region of right margin of pallial cavity, anterior one third of pallial right margin without internal structures (Fig. 17E); gill filaments triangular with tip about central (Fig. 17B); osphradium with left filaments smaller and fewer than right filaments.

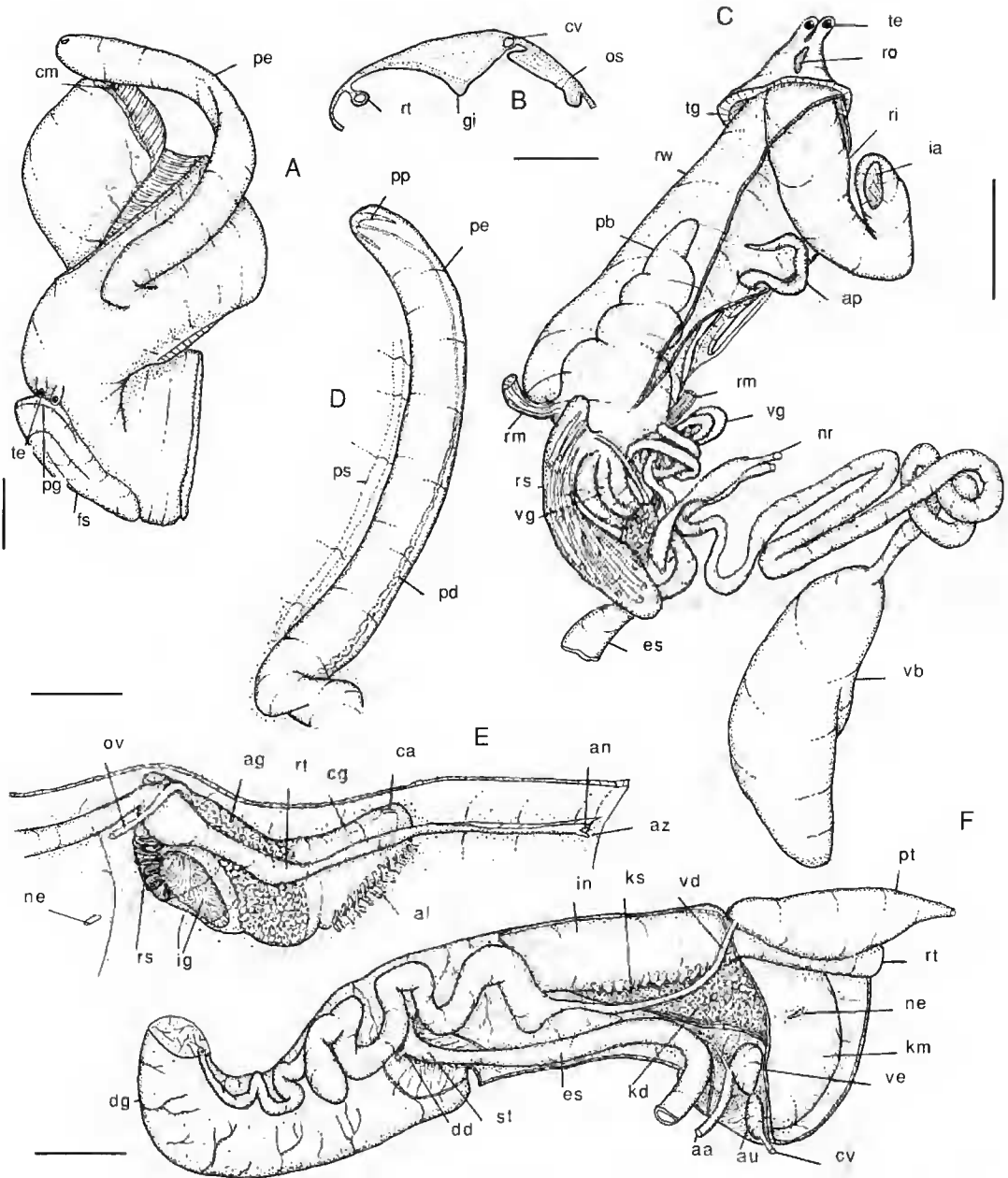


FIG. 17. — *Terebra crassireticula* n. nom., anatomy: A, ♂ head-foot, mantle removed; B, pallial cavity roof, transverse section of its middle region; C, head and foregut removed, ventral view, rhynchodoal wall partially opened with some internal structures exposed; D, penis and adjacent area of head-foot, dorsal view; E, pallial oviduct and adjacent structures, ventral view; F, part of visceral mass and a short portion of adjacent pallial cavity, part of digestive gland adjacent to stomach removed, kidney and pericardium opened, internal surface exposed. Scale bars: 0.5 mm

Circulatory and excretory systems (Fig. 17F)

Heart of proportionally small size, similar in position to that of preceding species. Kidney of

almost one third whorl, flattened, located in right region of posterior limit of pallial cavity. Kidney with flattened inner chamber separating

two glandular masses. Dorsal glandular mass thin, white, with several, irregular glandular acina. Ventral right mass border attached to rectum, very thin, with several transverse folds. Nephridial gland small, pale cream, section triangular, bordering dorsal margin of membrane between kidney and pericardial chambers. Nephrostome a transverse slit in middle region of membrane between kidney and pallial cavity.

Digestive system (Figs 6C; 7F; 17C, F)

Rhynchodeal introvert occupies about half of remainder of foregut length, cylindrical (Fig. 17C), double walls thick and muscular. Distal aperture of rhynchodeal introvert (rhynchostome) large, preceded by a moderately thickened sphincter. Rhynchodeal wall very thin, transparent, covers inner surface of anterior half of haemocoel as does that of preceding species (Fig. 17C). Accessory proboscis structure small, white, long, connected to rhynchodeal wall in middle region of its left side and attached to inner surface of haemocoel by small ligaments (Fig. 17C: ap); inner region muscular, outer region glandular and irregular. Proboscis conical, clearly shorter than rhynchocoel, connected airtight posterior limit to rhynchodeal wall and retractor muscle; gripping tooth at its tip, similar to *H. cinerea*. Buccal mass spherical, with inner and outer organization similar to that described for *H. cinerea*. Radula (Fig. 6C) described by Simone & Verissimo (1995: 464, fig. 8), each tooth about 280 µm long. Salivary glands not hemi-spherical, so a deformed glandular mass. Venom gland very long, narrow and convolute, about half anterior and half posterior to nerve ring, distal region broader than proximal region, but apparently with same inner tissue organization. Muscular bulb elliptical, short, almost circular in section; two inner muscular layers, inner layer of about half thickness of outer layer. Inner surface of buccal mass similar to that of preceding species. A sketch of foregut structures shown in Figure 7F. Oesophagus a long, narrow tube (Fig. 17F), flattened and with smooth inner surface in its anterior region, narrow, with several longitudinal folds in its posterior region; no developed inner glands. Stomach (Fig. 17F) simple, curved, located half a whorl posterior to kidney,

immersed in digestive gland. Duct to digestive gland single, located in middle, ventral region of stomach. Digestive gland of about 5.5 whorls posterior to stomach, beige. Intestine broad, with thin walls, inner surface almost smooth, runs to left of and ventral to kidney. Other details in Simone & Verissimo (1995: 464, fig. 7).

Genital system (Fig. 17A, D-F)

Male. Testis rather short, located in columellar region of second whorl posterior to stomach. Visceral vas deferens very broad at level of half a whorl before kidney, with thick, convoluted walls (Fig. 17F). In renal level vas deferens narrows abruptly, runs near columella and exits to pallial cavity in its posterior right region. Prostate a thick-walled, broad, short tube of about half length of rectum, without detectable aperture (Fig. 17F). Vas deferens runs along floor of right margin of pallial cavity, in its anterior region stays immersed in head tegument; before its entrance to penis, vas deferens thicker. Penis (Fig. 17A, D) rather short – little more than half length of pallial cavity, flattened; with about uniform width along its length. Penis duct very narrow, clearly sinuous in its proximal half, running near left penis margin. Penis distal end with a concavity turned to right, in its centre a rather large papilla where penis duct opens.

Female. Visceral oviduct very narrow, running close to columella, with a small gono-pericardial aperture; inserted in pallial gonoduct at right of albumen gland. Entire pallial oviduct very short – about half length of rectum (Fig. 17E). Ingesting gland elliptical, circular in section, with muscular walls; receptaculum seminis, connecting ingesting gland to oviduct, narrow, long and convolute, located dorsal to oviduct. Albumen and capsule glands connected to each other, with a single flattened duct which opens in right region of anterior extremity close to columella. Terminal pouch lacking.

Terebra gemmulata Kiener, 1839
(Figs 1G, H; 3D, E; 7G; 8C; 13A; 18-20)

Synonymy – cf. Matthews *et al.*, 1975: 90 and Bratcher & Cernohorsky, 1987: 148.

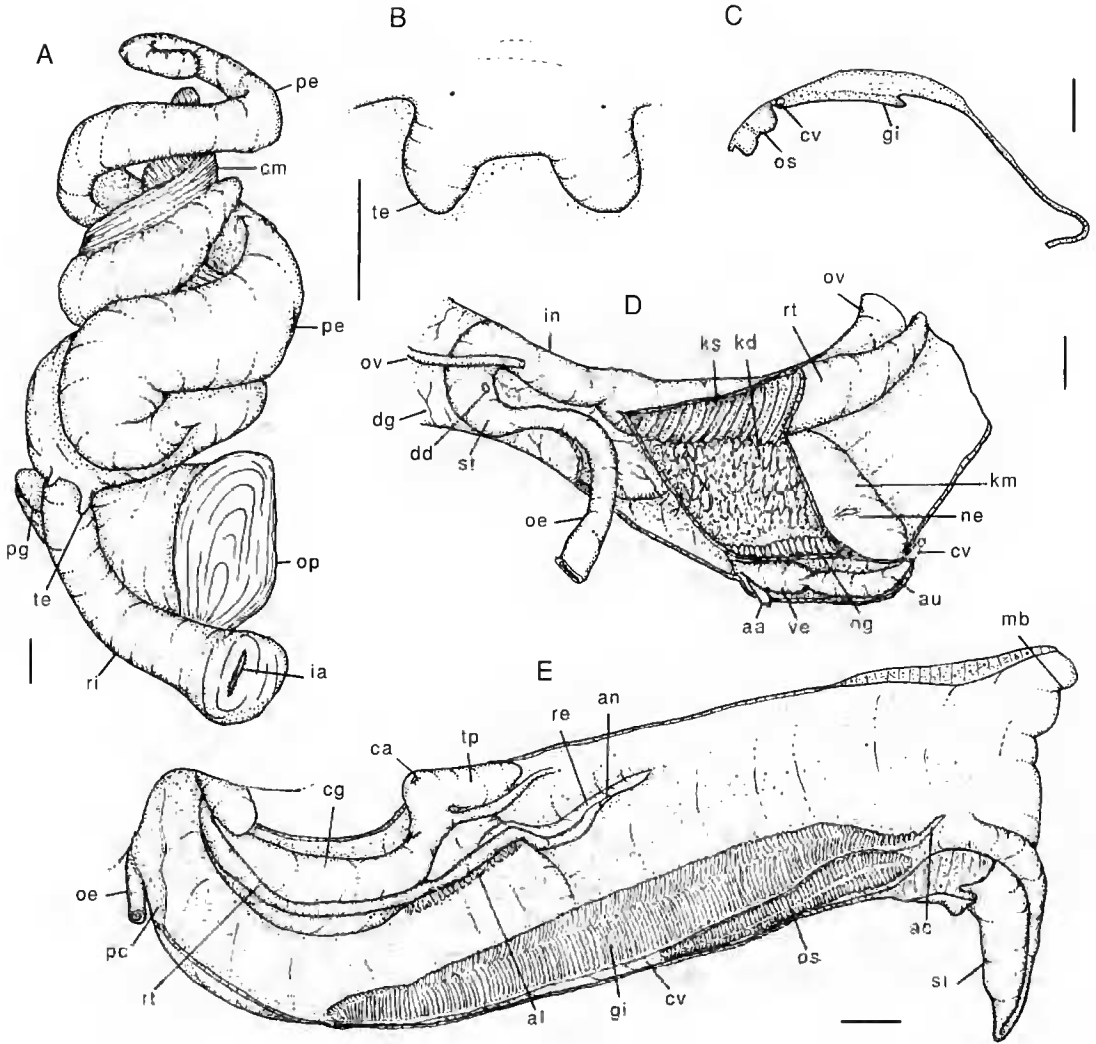


FIG. 18. — *Terebra gemmulata*, anatomy, A, ♂ head-to-foot, mantle removed, introvert partially protracted; B, detail of A in region of tentacles in a specimen with visible eye (generally they are not visible); C, transverse section of middle region of pallial roof; D, anterior region of visceral mass, ventral view, digestive gland near stomach partially removed, kidney and pericardium opened, their internal region exposed; E, pallial organs, ventral-internal view. Scale bars: A, E, 1 mm; B-D, 0.5 mm.

Others: *Terebra gemmulata* – Rios 1985: 130 (fig. 587); 1994: 180 (fig. 836).

MATERIAL EXAMINED. — **São Paulo**, Brazil, off Santos Bay, 32 m, 14.IV.1969, 2 ♀♀ (MZSP 28392).

Rio Grande do Sul, Brazil, off Mostardas, RV W. Besnard, stn 430, 31°33'S, 51°05'W, 21 m, 5.XI.1968, 1 ♂ (MZSP 19325).

DISTRIBUTION. — From Rio de Janeiro, Brazil to San Matías Gulf, Argentina.

HABITAT. — From 15 to 90 m deep. Sandy substrates.

MEASUREMENTS. — MZSP 28392: 37.9 × 7.8 mm; MZSP 19325: 32.0 × 7.7 mm.

DESCRIPTION

Shell (Figs 1G, H; 13A)

Shell description found in Matthews *et al.* 1975: 90-91 (figs 7, 8); Bratcher & Cernohorsky 1987: 148 (fig. 166a-e).

Head-foot (Figs 8C; 18A, B; 19A)

Colour homogeneous yellowish cream. Head weakly differentiated from head-foot axis (Fig. 18A). Tentacles very short, dorso-ventrally flattened, tip rounded (Fig. 18B). Eyes lacking in some specimens or extremely small, dark, located at tentacle base (Fig. 8C). Basal, proximal introvert aperture rather broad, transverse, anterior and ventral to tentacles (Fig. 19A). Foot occupying almost half a whorl, without divisions; sole with folded borders. Columellar muscle of two whorls, rather thick (Fig. 18A). Males with very large penis in central-right region posterior to head.

Operculum (Figs 3D, E; 18A)

Large, unguiculate, brown, nucleus terminal (Fig. 3D, E). Occupying entire shell aperture (Fig. 18A).

Mantle organs (Figs 18C, E; 20D)

Mantle border simple, not pigmented. Siphon well-developed, yellowish cream, with smooth borders (Fig. 18E). Mantle cavity of about 2.5 whorls. Osphradium elliptical, very long, about half of gill length; with several uniform filaments on both sides of osphradial ganglion; right filaments similar in size to left filaments; anterior half broader than posterior, which tapers gradually. Gill narrow and long, about seven tenths of pallial cavity length; anterior end rather far from mantle border, with only a short portion of ctenidial vein present, in form of a very small septum; filaments begin gradually some distance from anterior end (Fig. 18E); each filament triangular, low, apex located at the right, margin almost straight (Fig. 18C); gill posterior extremity very far from pericardium, a long portion of ctenidial vein free from gill filaments (Fig. 18E). Ctenidial vein narrow and uniform all along its length, except for its broader anterior extremity. A proportionally broad space between gill and rectum. Hypobranchial gland thin, located in posterior half of cavity, at left of rectum, pale cream. Anal gland with a few slender, irregular acina immersed in right margin of hypobranchial gland in anterior half of rectum, but far from anus (Figs 18E; 20D), purple. Pallial gonoducts run along right margin of posterior half of pallial

cavity, attached to pallial floor. Rectum narrow, lying ventral to and left of pallial gonoducts; in females, in its middle region it separates from oviduct on margin of a pallial septum (Figs 18E, 20D). Anus far from anterior extremity of pallial oviduct in females or prostate in males; bears a small papilla. Anterior third of pallial right margin without internal structures.

Circulatory and excretory systems (Figs 18D; 20A)

Heart of small size, position similar to those of preceding species. Kidney of almost half a whorl, flattened, located in right region of posterior limit of pallial cavity. Kidney with a large wide inner chamber separating two main glandular masses. Dorsal glandular mass rather thick and bearing several lobed folded acini. Ventral right mass thin, bordering and attached to rectum, bearing several transverse, uniform folds. Both kidney masses pale cream. Nephridial gland well-developed, pale cream, triangular in section, bordering dorsal margin of membrane between kidney and pericardial chambers (Fig. 18D; ng). Nephrostome a transverse slit in middle region of membrane between kidney and pallial cavity.

Digestive system (Figs 7G; 18A, D; 19; 20A)

Rhynchodeal introvert very long, about 1.5 time rhynchocoel length (coiled in retracted condition), cylindrical (Figs 18A; 19A, B, E), muscular walls thick, separated into two layers connected to one another by several, uniformly distributed, transverse muscle fibres (Fig. 19D). Outer layer (in retracted condition) mainly of longitudinal fibres and inner layer mainly of circular fibres. Distal aperture of rhynchodeal introvert (rhynchostome) large and with a terminal muscular sphincter; in one side a pair of longitudinal folds (Fig. 19D). The two layers of introvert walls do not glide over one another when introvert is protracted, so whole wall is evaginated. Rhynchodeal wall very thin, transparent, covering inner surface of anterior half of haemocoel in preceding species (Fig. 19). Several small muscle fibres connect rhynchodeal walls with inner surface of haemocoel (more concentrated in anterior extremity) and with other foregut structures; two muscles, in particular, more developed: one pair posterior to nerve ring, connecting oesophagus

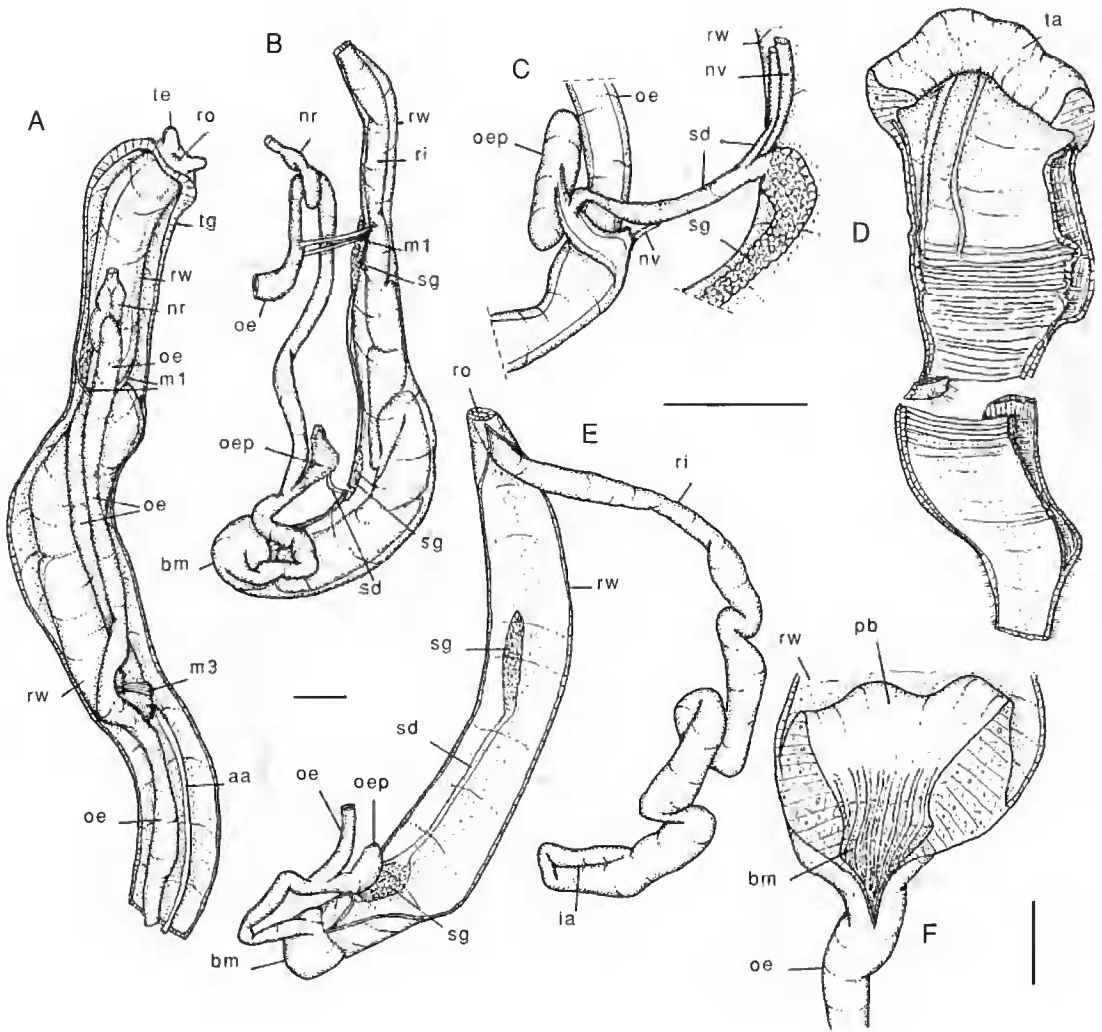


FIG. 19. — *Terebra gemmulata*, anatomy; **A**, head and haemocoel, ventral view, foot and columellar muscle removed; **B**, foregut removed from haemocoel, left view, oesophagus partially deflected; **C**, detail of **B** in proximal region of oesophagus, part of rhynchoideal wall also shown; **D**, rhynchoideal introvert, details of its internal surface (when retracted) exposed by means of longitudinal section, distal (upper) and proximal (down) extremities, double walls clear at right side; **E**, foregut removed, rhynchoideal wall sectioned longitudinally, introvert reflected, salivary glands seen by transparency; **F**, detail of posterior region of rhynchoideal wall and vestigial proboscis opened longitudinally, internal surface exposed. Scale bars: 1 mm.

with dorsal wall of haemocoel, embracing also rhynchoideal wall (Fig. 19A, B: m1), and another muscle in posterior extremity of rhynchoideal, connecting oesophagus to buccal mass (Fig. 19A: m3). Proboscis very small, reduced, present only as muscular ring around anterior surface of buccal mass (Fig. 19B-F). Buccal mass spherical. Pair of retractor muscles reduced. Radular sac wan-

ting. Salivary glands divided into two separated masses (Fig. 19B-E), one of them located anteriorly and the other posteriorly, connected with each other by a narrow duct inserted in oesophagus near posterior salivary gland, where in some specimens there is a small elliptical pouch (Fig. 19C: ep) (some specimens lack this pouch). The exact position of the salivary glands also

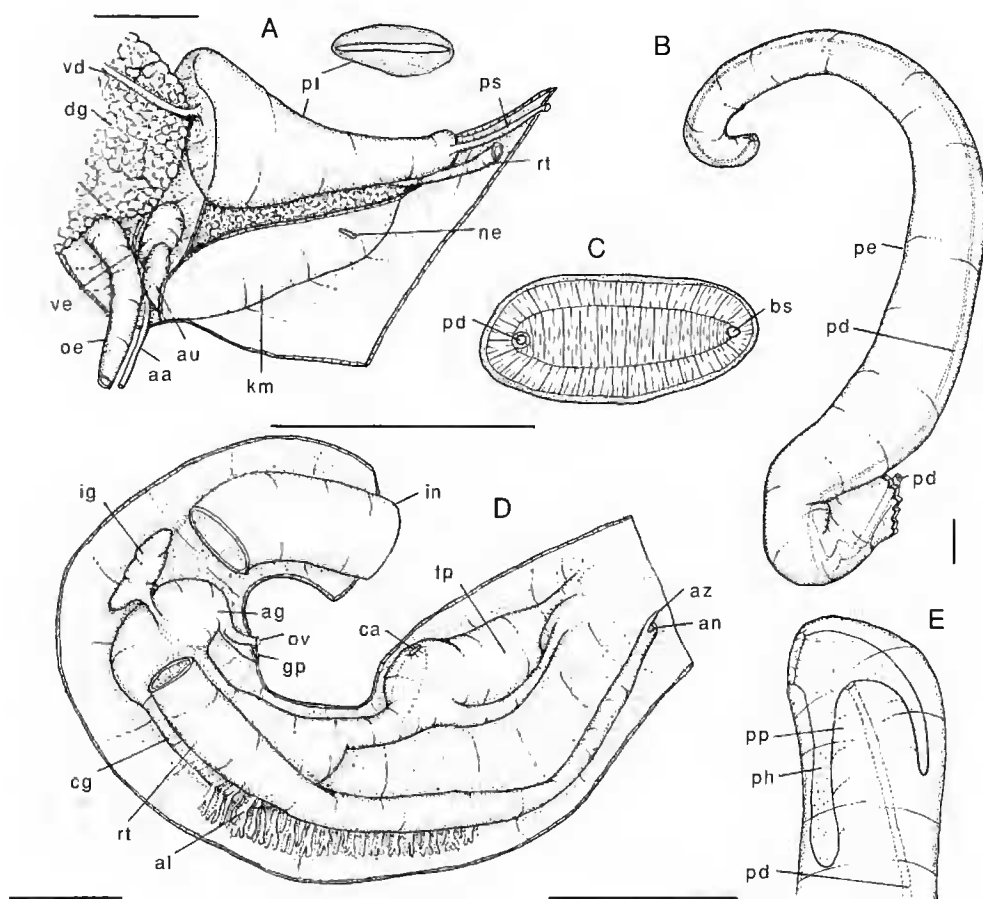


FIG. 20. — *Terebra gemmulata*, anatomy; **A**, anterior region of visceral mass and adjacent region of pallial cavity, ventral view, pericardium and kidney partially dissected; **B**, penis, ventral view; **C**, penis, transverse section in its middle region; **D**, pallial oviduct and adjacent areas, ventral view; **E**, penis, detail of its distal extremity seen as if transparent. Scale bars: 1 mm.

varies among specimens, it can be more anterior or posterior, close to one another, etc. Venom gland and muscular bulb absent. A sketch of foregut structures shown in Figure 7F. Inner surface of buccal mass with several longitudinal low folds which continue into oesophagus (Fig. 19F). Oesophagus a long, narrow tube, running with some coils to anterior region where it passes through nerve ring, twists and returns to posterior (Fig. 19A, B), this position is maintained by a small pair of muscles m1; interior glands no developed; posterior region with internal longitudinal folds until near stomach. Stomach simple, curved (Fig. 18D), located half whorl

posterior to kidney, immersed in digestive gland. Duct to digestive gland single, located in middle, ventral region of stomach. Digestive gland of about 5,5 whorls posterior to stomach and half a whorl anterior to it (Figs 18D; 20A), beige. Intestine broad, with thin walls and an almost smooth internal surface; runs left and ventral to margin of kidney. Rectum and anus described above.

Genital system (Figs 18A, D, E; 20)

Male. Testis similar to that of preceding species. Visceral vas deferens runs close to columella. Prostate thick-walled, conical, broad and short,

located in right region of kidney and not in pallial cavity (Fig. 20A), except for a short anterior portion; visceral vas deferens inserted in middle of prostate posterior surface. Pallial vas deferens runs along right margin of floor of pallial cavity, in its anterior region remaining immersed in head tegument. Penis very long, longer than pallial cavity length (distal region stays twisted) (Fig. 18A), flattened (Fig. 20B); narrowing gradually; penis duct very narrow, nearly straight, near left margin of penis (Fig. 20B, C); on its opposite side (right) a differentiable blood sinus (Fig. 20C). Penis distal end with a deep concavity turned to right and with a small aperture; in its centre a rather large papilla in which penis duct opens (Fig. 20E).

Female. Ovary similar in position to testis. Visceral oviduct very narrow (Fig. 18D), running close to columella, inserted in pallial oviduct in its right posterior extremity; with a small gonopericardial duct. Albumen gland short, thick-walled, white (Fig. 20D). Ingesting gland rather triangular, located in left posterior region of pallial oviduct; receptaculum seminis long, crossing limit between albumen and capsule glands, inserting in right margin of pallial oviduct. Capsule gland yellow, long – about half of total pallial oviduct length, cylindrical, with a central, flattened duct which opens in a small slit at right of terminal pouch base in tip of an outstanding elevation (Figs 18E; 20D). Terminal pouch broad, with a longitudinal furrow turned to left and opened; left lip of this aperture much smaller than right one; occupies almost half of total length of pallial gonoduct (Fig. 20D).

Terebra leptapsis n. sp.

(Figs 7F; 12B, C; 13F; 14C, G; 21; 22)

TYPE MATERIAL. — Holotype: MZSP 28704. Paratypes: 1 specimen MZSP 28705; 13 shells MZSP 28706, all from type locality.

OTHER MATERIAL. — **Rio de Janeiro**, Brazil, off Cabo Frio, RV W. Besnard, stn 1485, 22°39'S, 41°33'W, 52 m, 10.III.1971, 7 shells (MZSP 19404). — Stn 1483, 23°00'S, 42°10'W, 64 m, 10.III.1971, 3 shells (MZSP 19403). — Off Rio de Janeiro, stn 1476, 23°06'S, 42°54'W, 59 m,

9.III.1973, 9 shells (MZSP 19402). — Ilha Grande, outer trawl, 50 m, VI.1971, 1 shell (MNRJ 3656).

São Paulo, Brazil, off Ubatuba, RV Veliger, stn 26, 23°30'S, 44°54'W, 42 m, 21.IV.1986, 1 specimen (MZSP 28710); stn 17, 23°34'S, 44°48'W, 44 m, 22.I.1986, (MZSP 28709); stn 31, 23°53'S, 45°09'W, 38 m, 10.VII.1986, 1 shell (MZSP 28703). — RV W. Besnard, stn 4851, 23°36'S, 44°46'W, 48 m, 16.XII.1985, 13 shells (MZSP 28699), 7 shells (MZSP 28702); 23°36.2'S, 44°39.5'W, 50 m, 26.VII.1986, 1 shell (MZSP 28701). — Off Santos Bay, 32 m, 14.IV.1969, 1 shell (MZSP 28394). — 23°36'S, 44°46'W, 48 m, 16.XII.1985, 1 specimen (MZSP 28395). — No locality, *Conversul-1*, NOAS expedition, stn 4594, loc. 4511, 30 m, 25.VIII.1977, 1 shell (MZSP 28700).

TYPE LOCALITY. — Brazil, Rio de Janeiro, Campos Bay (RV *Austrogaroupa*).

ETYMOLOGY. — The specific epithet refers to the narrow reticulate sculpture of the shell, from Greek *leptos* (tenuous) and *hopsis* (net).

DISTRIBUTION. — From Rio de Janeiro to São Paulo, Brazil.

HABITAT. — Sandy substrates; from 32 to 64 m depth.

MEASUREMENTS. — In millimeters, followed by number of axial and spiral ribs in penultimate whorl: holotype, 15.9 × 4.0, 27, 6; paratype MZSP 28705, 15.7 × 3.7, 27.5.

REMARKS

The holotype and paratypes MZSP 28705, 28706 were collected at several points of Campos Bay, no precise locality or depth was given. Even so, they are chosen due to their perfect shells, in all other available lots the shells are eroded or broken. The single preserved specimen (MZSP 28395) had its shell broken for anatomical study.

DIAGNOSIS

Shell small, with protoconch of two whorls; sculptured by narrow axial and spiral ribs, of equal prominence, about thirty axial rib in penultimate whorl. Tentacles separated from one another and with eyes at tip. Foregut complete, with broad, flattened accessory proboscis structure. Penis long and narrow.

DESCRIPTION

Shell (Fig. 12B, C; 13F; 14C, G)

Long, slender, turritiform, small (about 15 mm high), with up to thirteen convex whorls, pale cream. Protoconch (Fig. 14C) of two whorls, convex, smooth; junction with teleoconch clear. Sculpture of first teleoconch whorls (Figs 12B, C; 14G) mainly of narrow, uniform axial ribs, each with a subsutural node; gradually spiral ribs appear, six to seven on penultimate whorl, with about same width as axial ribs; a small node at intersection of spiral and axial ribs; subsutural nodes prominent; about thirty axial ribs on penultimate whorl. Aperture simple (Fig. 13F); outer lip with cut-edge; inner lip smooth, sigmoid. Canal short, open, curved.

Head-foot (Figs 21B, C; 22A)

Colour homogeneous clear beige. Head weakly differentiated from head-foot axis (Fig. 21B). Tentacles short, dorsoventrally flattened, tip rounded, well-separated from each other (Figs 21B, C; 22A). Eyes rather large, dark, located at tentacle tip. Basal, proximal introvert aperture narrow, transverse, anterior and ventral to tentacles. Foot occupying almost half a whorl, without divisions; furrow of pedal glands anterior. Columellar muscle of about 1.5 whorls, rather thick. Male with penis inserted very posteriorly (Fig. 21B).

Operculum

Large, unguiculate, pale brown, nucleus terminal. Occupying entire shell aperture (Fig. 21B).

Mantle organs (Fig. 21A, E)

Mantle border notched near siphon base and some papilla-like digitations to right and left of it. Siphon well-developed, long, clear beige, with smooth edges. Mantle cavity of about two whorls. Osphradium, elliptical long, about same length as gill; with several filaments; right filaments larger and more numerous than left filaments; anterior two thirds of osphradium with filaments more widely spaced, posterior one third with filaments closer. Gill narrow and rather short, about half length of pallial cavity; anterior end rather close to mantle border, a portion of ctenidial vein with length about one third that of remainder of gill,

without filaments; filaments begin gradually after this; each filament triangular, apex nearly central, margins almost straight; filaments of anterior half of gill more widely spaced than those of posterior half; gill posterior end far from pericardium. Ctenidial vein narrow and uniform all along its length, except for its broader anterior extremity. A proportionally narrow space between gill and rectum. Hypobranchial gland thin, located in posterior half of cavity, at left of rectum, yellowish. Anal gland not differentiable. Pallial spermoduct run along right margin of posterior half of pallial cavity. Rectum narrow, lying ventral to and left of pallial spermoduct. Anus near anterior extremity of pallial spermoduct; bears no papilla. Anterior half of pallial right margin without interior structures.

Circulatory and excretory systems (Fig. 21F)

Heart of small size, similar in location to those of preceding species. Kidney similar to that of *T. crassireticula*, except in having ventral right mass (bordering rectum) with transverse folds taller than in *T. crassireticula*. Nephridial gland also similar to that of *T. crassireticula*. Nephrostome a transverse slit in middle region of membrane between kidney and pallial cavity.

Digestive system (Figs 7F; 21D, F; 22A, B)

Rhynchodeal introvert occupies about one third of remainder of foregut length, cylindrical, thick-muscular, walls double (Fig. 22A). Distal aperture of rhynchodeal introvert (rhynchostome) wide. Internal rhynchodeal wall very thin, transparent, covers internal surface of anterior half of haemocoel as in preceding species (Fig. 22A, B). Accessory proboscis structure long (about one third length of total foregut structures), clear brown, flattened, base broader, gradually tapers into a rather rounded tip; connected to rhynchodeal wall in middle region of its left side (Fig. 22A, B); no ligament connecting it with internal surface of haemocoel; internal region muscular, outer region glandular. Proboscis conical, of about same length as rhynchocoel; its base connected by small muscle fibres to rhynchodeal wall and to several pairs of retractor muscles. Buccal mass long (Fig. 22B), with internal and external organization similar to that described for

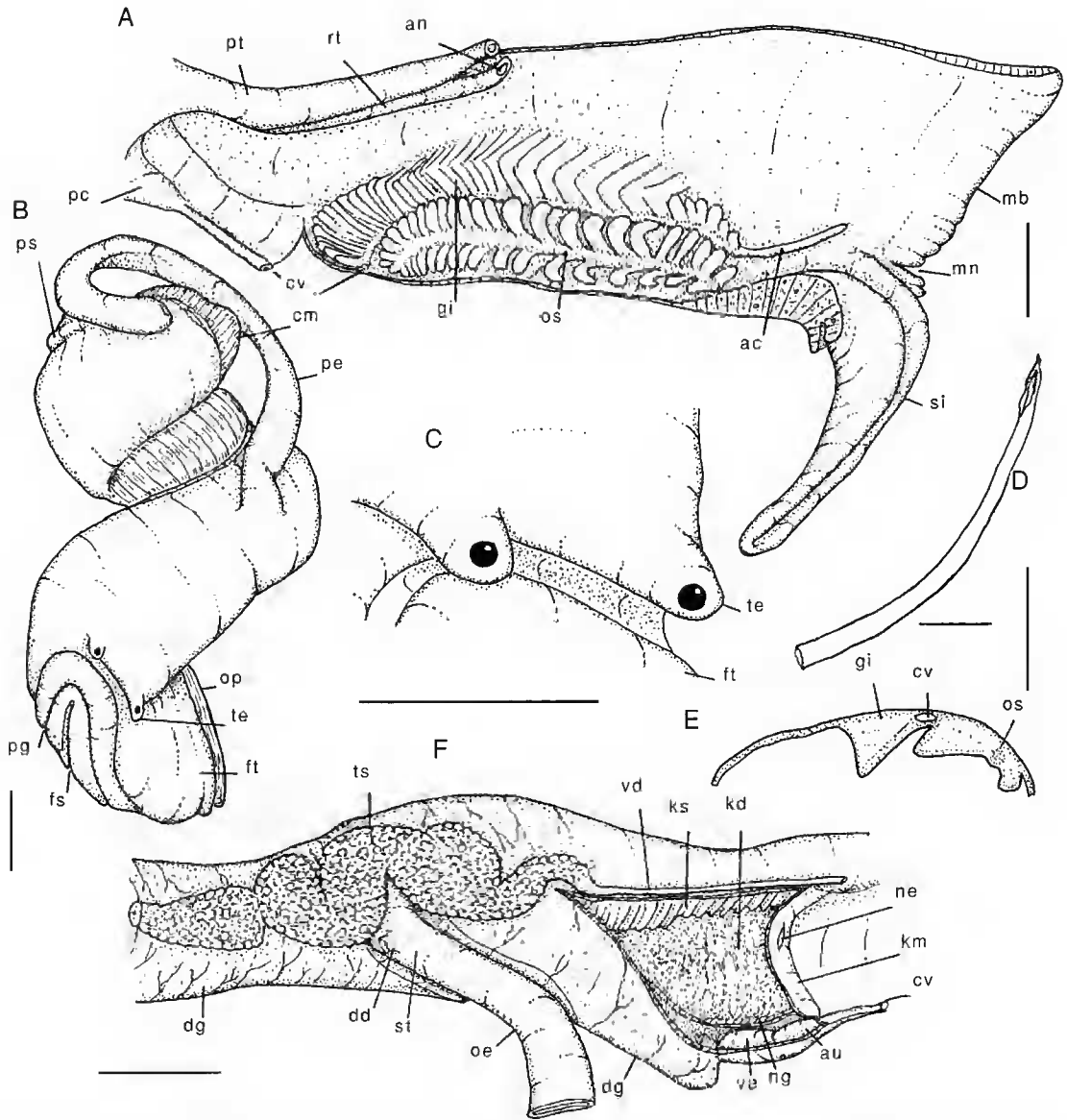


FIG. 21. — *Terebra leptapsis*, n. sp., anatomy; A, pallial organs, ventral-internal view; B, head-foot of male, mantle removed; C, same, detail of tentacles region; D, radular tooth; E, pallial cavity roof, transverse section in its middle region; F, last whorls of visceral mass, ventral view, kidney and pericardium opened, adjacent region of pallial cavity also shown. Scale bars: 0.5 mm.

T. cinerea. Radula similar to that of *T. crassireticula* but with clearly longer and more slender teeth (Fig. 21D). Salivary glands amorphous, their ducts similar to those of preceding species. Venom gland very long, narrow and convolute, about one third anterior and two thirds posterior

to nerve ring. Muscular bulb elliptical, long (Fig. 22A), section almost triangular. Internal surface of buccal mass similar to that of preceding species. A sketch of foregut structures shown in Figure 7F. Oesophagus long and narrow, flattened, with smooth internal surface. Stomach

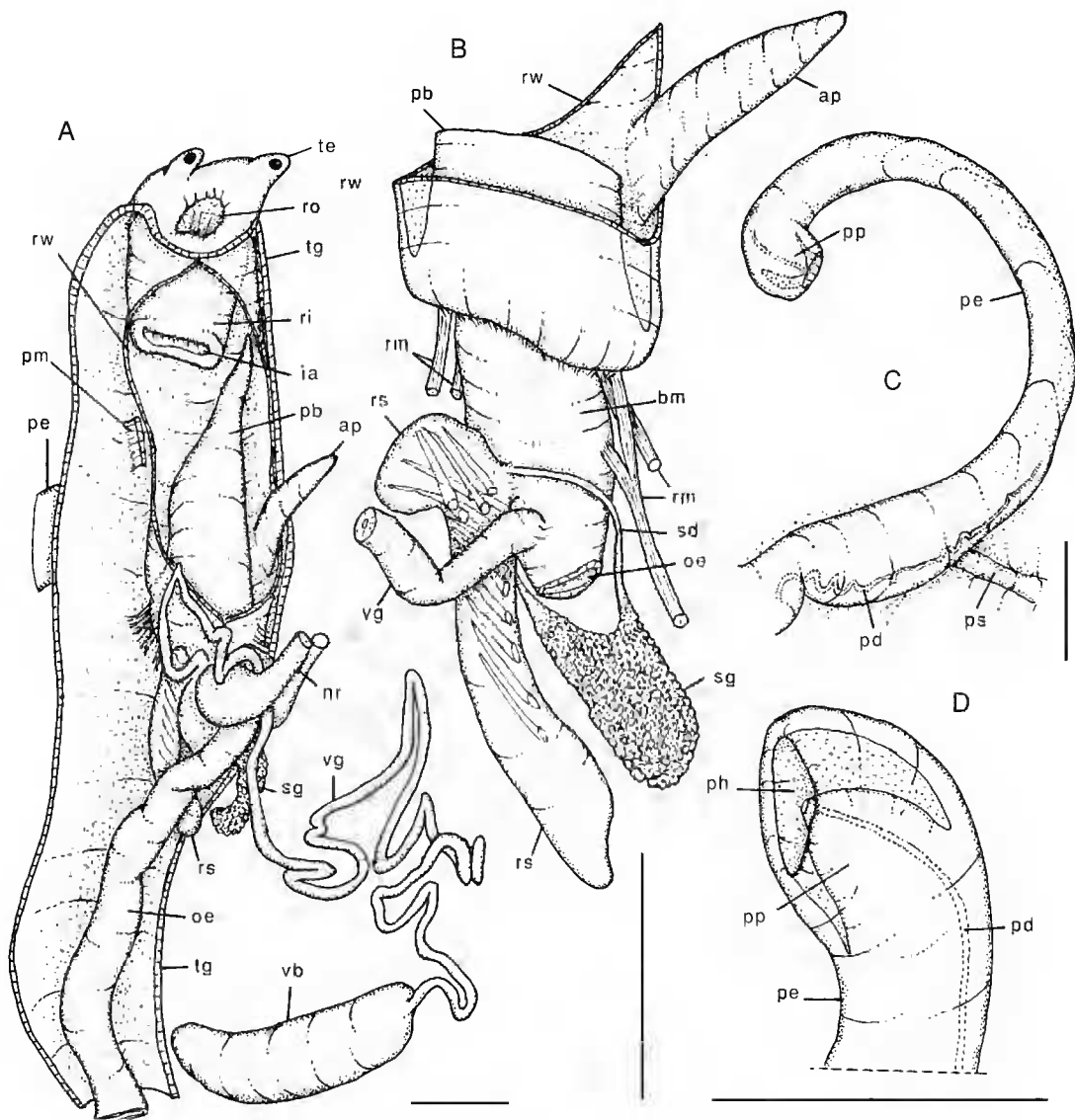


FIG. 22 — *Terebra leptapsis* n. sp., anatomy; **A**, head and haemocoel, ventral view, foot and columellar muscle removed, rhynchodeal wall partially opened longitudinally, accessory proboscis structure (ap) reflected; **B**, foregut (posterior extremity) and buccal mass, rhynchodeal wall, proboscis, venom gland and oesophagus only shown in their basal region; **C**, penis, ventral view, part of pallial vas deferens also shown; **D**, penis, detail of its distal extremity as if a transparent structure. Scale bars: 0.5 mm.

simple, curved (Fig. 21F), located half a whorl posterior to kidney, immersed in digestive gland. Duct to digestive gland single, located in middle, ventral region of stomach. Intestine broad, with thin walls, with an almost smooth internal surface, running left and ventral to kidney. Rectum and anus described above.

Genital system (Figs 21A, B, F; 22C, D) Only male examined. Testis similar to those of preceding species (Fig. 21F). Visceral vas deferens narrow, almost straight, running ventral to kidney (Fig. 21F). Prostate thick-walled, narrow (Fig. 21A). Pallial vas deferens runs along right margin of floor of pallial cavity, in its anterior

region staying immersed in head tegument; before its entrance to penis, vas deferens thicker. Penis narrow and long, about same length as palial cavity (Fig. 21B); origin very posterior, far from tentacles; about uniform width along its length (Fig. 22C). Penis duct very narrow, clearly sinuous in its proximal half, running near left penis margin. Penis distal end with a concavity turned to right (Fig. 22D), in its centre a rather large papilla where penis duct opens.

DISCUSSION

Shell and soft parts characters of *T. leptapsis* are similar to those of *T. crassireticula*, from which *T. leptapsis* differs in having: (1) protoconch with one more whorl (two rather than one whorl); (2) sculpture more delicate; (3) more axial ribs (30 on penultimate whorl in contrast with about 18 in *T. crassireticula*); (4) cephalic tentacles far apart; (5) notch in mantle border at base of siphon; (6) accessory proboscis structure broader, shorter and without ligament in its base; (7) venom gland with two thirds of its length posterior to nerve ring rather than a half, and (8) penis narrower and longer. Both differ from *T. doellojuradoi* Carcelles (1953: 14, fig. 21) (Bratcher & Cernohorsky 1987: 164-166, fig. 194a, b) in being longer, more slender, differently sculptured (see below) and in the absence of a columellar callus. Moreover, *T. doellojuradoi* has about 23 axial ribs on the last whorl (according to Carcelles 1953 and Bratcher & Cernohorsky 1987), while *T. crassireticula* has fewer than twenty and the axial and spiral ribs are broader; *T. leptapsis*, in contrast, has almost thirty axial ribs and both axial and spiral ribs are narrower than those of the other two species. The occurrence of *T. doellojuradoi* on the Brazilian coast is still obscure, in São Paulo and Rio de Janeiro coasts (the northern limit of its range according to Rios 1994) no specimen of this species was found, although several specimens of *T. crassireticula* and *T. leptapsis* were identified as *T. doellojuradoi*. The type locality of *T. doellojuradoi* is Uruguay and it probably occurs on the southern Brazilian coast, but a more precise definition of its geographic distribution depends on further studies.

Terebra taurina (Lightfoot, 1786) (Figs 6E, G; 7C; 8G; 13D; 14A; 23; 24)

Synonymy — cf. Matthews *et al.* (1975: 87) and Bratcher & Cernohorsky (1987: 128).

Others: *Terebra taurina* — Rios 1985: 130 (fig. 589). — 1994: 180 (fig. 840).

MATERIAL EXAMINED. — **Bahia**, Brazil, Salvador, Baía de Todos os Santos, 2 m, II.1997, B. Albuquerque coll., 1 ♂ (MZSP 28711).

Rio de Janeiro, Brazil, Baixos de São Tomé, RV *Muriel March*, IX.1994, 2 ♂ ♂, 2 ♀ ♀ (IBU-FRJ 8765).

DISTRIBUTION. — From Florida, USA, to Santa Catarina, Brazil.

HABITAT. — Infratidal, sandy or sandy mud substrates.

DESCRIPTION

Shell (Fig. 14A)

Adequate description found in Matthews *et al.* 1975: 87-90 (figs 1-6); Bratcher & Cernohorsky 1987: 128 (fig. 142a-d; pl. B, fig. 8). It is notable for the presence of a well-developed columellar fold (Fig. 13D) at the level of the inner lip.

Head-foot (Figs 23A, B, C; 24A)

Colour homogeneous clear brown. Head immersed (Fig. 23A). Tentacles moderately developed, dorso-ventrally flattened, tip rounded, broad (Figs 23B, C; 24A). Eyes dark, located at tip of tentacles. Basal, proximal introvert aperture a broad slit just ventral to tentacles. Foot long, a little more than half a whorl. Furrow of pedal gland anterior. Columellar muscle of about two whorls, thick, with an obvious central-running furrow due to shell columellar fold.

Operculum (Fig. 23A)

Unguiculate, pale brown, rather thick, nucleus terminal. Occupying entire shell aperture (Fig. 23A).

Mantle organs (Fig. 23D-F)

Mantle border simple, not pigmented. Siphon well-developed, pale cream, borders smooth. Mantle cavity very deep, extending about 2.5 whorls. Osphradium bipectinate, elliptical, long, about one third of gill length; with several,

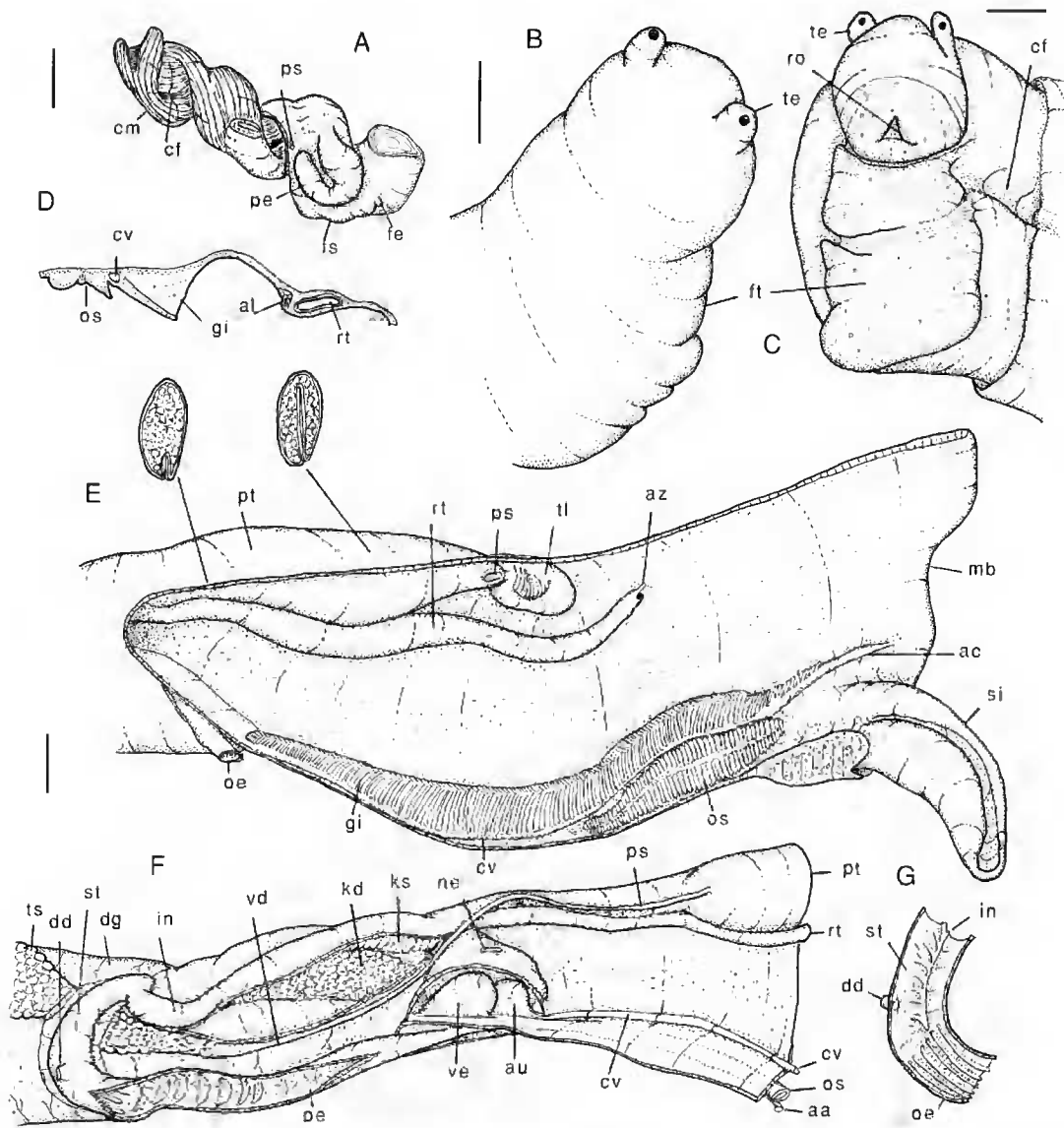


FIG. 23. — *Terebra taurina*, anatomy: **A**, ♂ head-foot, mantle removed; **B**, same, detail of head, dorsal view, foot partially removed; **C**, same, ventral view; **D**, pallial cavity roof, transverse section of its middle region; **E**, ♂ pallial organs, ventral-internal view, with two details of transverse section of indicated level of prostate; **F**, a whorl posterior and a whorl anterior to posterior extremity of pallial cavity, ventral view, digestive gland adjacent to stomach removed, distal region of oesophagus opened longitudinally with its internal surface (with septa) exposed, kidney and pericardium partially opened; **G**, ventral region of stomach opened longitudinally. Scale bars: A-D, 1 mm; E-G, 2 mm.

uniform filaments on both sides of osphradial ganglion; right filaments obviously larger than left filaments and with an angled projection covering ctenidial vein; each filament with smooth surface (not scalloped). Gill narrow, long, about

two thirds of pallial cavity length; anterior end near mantle border consisting only of ctenidial vein, in form of a small septum; filaments begin gradually at some distance from anterior end; each filament triangular, apex nearly central; gill

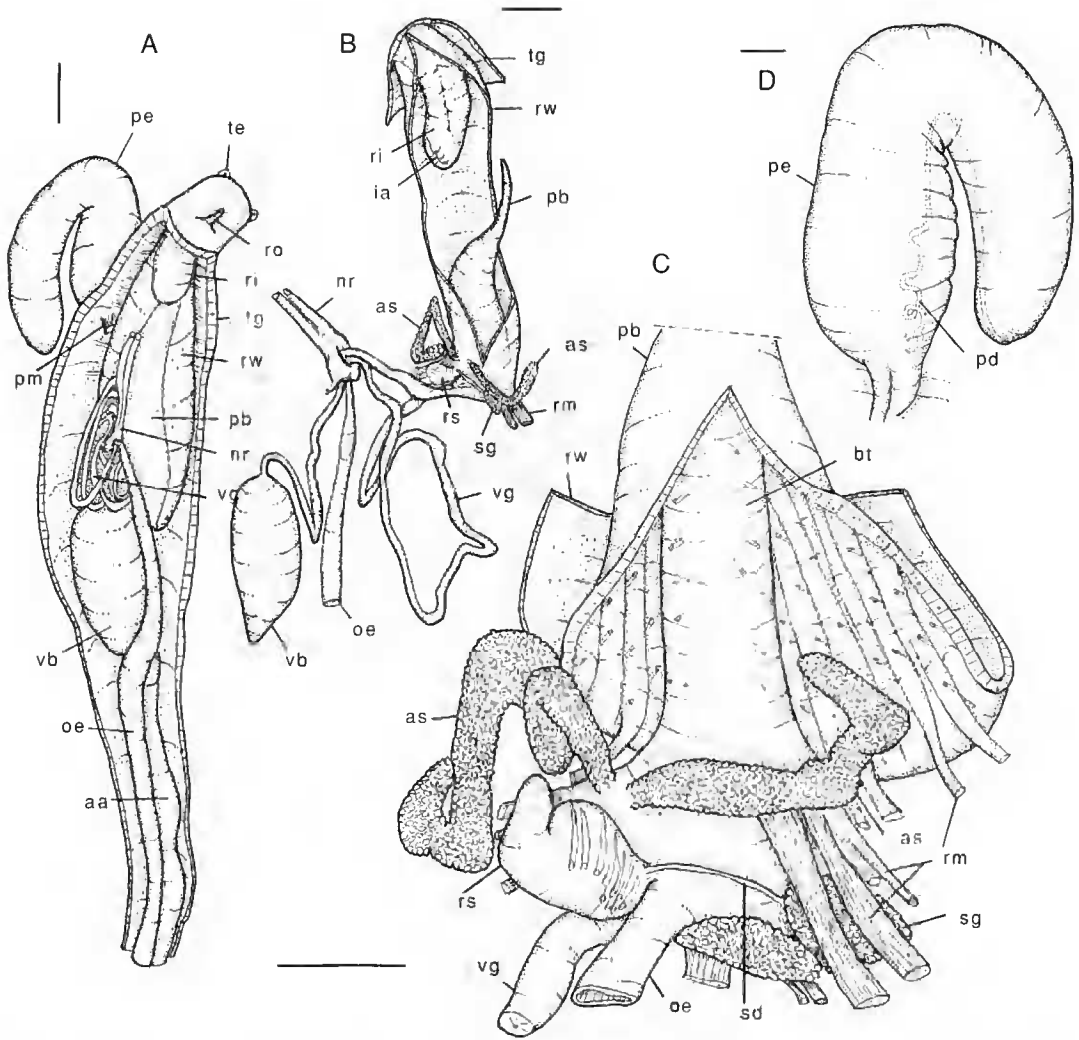


FIG. 24. — *Terebra taurina*, anatomy; **A**, head and haemocoel, ventral view, foot and columellar muscle removed; **B**, foregut removed, rhynchodeal wall opened longitudinally; **C**, detail of posterior extremity of foregut and buccal mass, base of proboscis and rhynchodeal wall opened longitudinally; **D**, penis, dorsal view. Scale bars: A, B, 2 mm; C, D, 1 mm.

posterior end very far from pericardium, with about one third of posterior region of pallial cavity free from gill. Ctenidial vein narrow and uniform all along its length, except for its broader anterior extremity; a very long portion without gill filaments in its posterior third. A proportionally broad space between gill and rectum. Hypobranchial gland thin, small, transparent, located in posterior half of cavity, at left of

rectum. Anal gland absent. Pallial gonoducts run along right margin of posterior half of pallial cavity, partly connected to pallial floor. Rectum narrow, lying at left of pallial gonoducts, its anterior region separated from gonoduct, attached to mantle (without septum). Anus located posterior to anterior third of pallial cavity. Anal papilla present. Anterior third of pallial right margin without interior structures.

Circulatory and excretory systems (Fig. 23F)

Heart similar to those of preceding species. Kidney of more than half a whorl, flattened, located in right region of posterior limit of pallial cavity. Kidney with two thin glandular masses, separated by broad chamber. Dorsal glandular mass thin, white, bearing a mosaic of irregular acini, clearly thicker in anterior region. Ventral glandular mass very thin, bordering rectum, semi-transparent, bearing several, uniform transverse folds. Nephridial gland narrow, white, triangular in section, transversely folded, borders dorsal margin of membrane between kidney and pericardial chambers. Nephrostome a transverse slit in middle-right region of membrane between kidney and pallial cavity.

Digestive system (Figs 6E, G; 8G; 23F, G; 24A-C)

Rhynchodeal introvert narrow and rather short (Fig. 24A, B). Distal aperture of rhynchodeal introvert (rhynchostome) a small transverse slit, preceded by a thin sphincter. Internal rhynchodeal wall very thin, transparent, covers internal surface of anterior half of haemocoel (Fig. 24A, C), connected to it by small muscle fibres mainly located in area from near rhynchostome to middle region. Proboscis conical, obviously shorter than rhynchocoel, its base connected by small muscle fibres and several pairs of small retractor muscles to rhynchodeal wall. Buccal mass spherical, with a long, broad buccal tube (Fig. 24C), with organization similar to that of *H. cinerea*, including gripping of tooth. Retractor muscles also insert in lateral surface of buccal mass. Radular sac short, curved, with several radular teeth, opens sub-terminally in ventral-middle region of buccal mass. Each radular tooth (Fig. 6E, G) curved, hollow, length about 900 μm ; base barbed, sinuous; basal region narrower, concave; middle region broad, nearly cylindrical, section circular (but not altogether fused); apical region sharply tapered, with a sinuous barb edging a long, narrow aperture. Salivary glands a pair of amorphous, white masses connected to each other; their ducts contour the oesophagus and insert in anterior and posterior region of base of radular sac aperture. Venom gland long and convolute, about two thirds anterior and one third posterior to

nerve ring (Fig. 24B); inserts in buccal mass close to and at left of radular sac aperture (Fig. 24C); no changes of glandular tissue along its length. Pair of accessory salivary glands long, flattened, inserted in buccal mass close to each other in region just anterior to insertion of radular sac (Fig. 24C: as); their ducts fuse after a short distance and run in outer buccal tube wall, opening in its anterior region. Muscular bulb rather long, elliptical, with broader proximal region and sharp distal extremity (Fig. 24A, B); two layers of muscular tissue, internal layer about half thickness of outer layer (Fig. 8G). Internal surface of buccal mass similar to that of *H. cinerea*. Oesophagus a long, narrow tube with smooth internal surface; in distal region, preceding stomach, six to seven transverse, shallow septa (Fig. 23F). Stomach similar to those of preceding species (Fig. 23F); internal surface with longitudinal folds in proximal region, and a single longitudinal fold in distal region, having several secondary transverse folds inserted along side, uniformly spaced (Fig. 23G). Duct to digestive gland single, located in middle, ventral region of stomach. Digestive gland of about 4.5 whorls posterior to stomach, beige. Intestine narrow, with thin walls, internal surface almost smooth; runs left and ventral to margin of kidney (Fig. 23F). Rectum and anus described above.

Genital system (Figs 23A, E, F; 24A, D)

Male. Testis in columellar side of visceral mass, narrows gradually anterior to stomach (Fig. 23F). Visceral spermoduct a continuation of testis, very narrow, runs ventrally, close to columella, between rectum and kidney. Pallial spermoduct runs along right margin of pallial cavity floor. Prostate only developed at some distance from posterior limit of pallial cavity, spermoduct is inserted in it subterminally (Fig. 23E, F). Penis long (Figs 23A; 24A), dorso-ventrally flattened, twisted; penis duct coiled in proximal region, very narrow, running near left margin of penis (Fig. 24D). Penis distal end rounded, simple, without papilla nor chambers; penis duct opens in tip.

Female. No female examined had well-preserved posterior genital structures; it was possible to note only a well-developed terminal pouch just posterior to anus.

Terebra spirosulcata

Simone & P. M. Costa, n. sp.

(Figs 1E, F; 3H; 6H, I; 7E; 8D, E; 13C; 25; 26)

Terebra doellojuradoi (?) — Matthews *et al.* 1975: 97 (figs 25-28) (not Carcelles 1953).*Terebra brasiliensis* — Bratcher & Cernohorsky 1987: 160 (figs 186c, d) (parr.) (not Smith 1873).TYPES MATERIAL. — **Rio de Janeiro.** Holotype: MNRJ 3657 (from type locality).

Paratypes: off Cabo Frio, 60 m, X.1993, 1 shell (MORG 32755). — Off Cabo de São Tomé, RV W. Besnard, stn IV, 22°06'S, 41°04'W, 16 m, 11.II.1969, 1 shell (MZSP 19596). — Stn III, 22°10.5'S, 41°59'0"W, 30 m, 2 shells (MZSP 25210). — Type locality 1 shell, (MNRJ 7570). — Off Cagaras Island, 30-40 m, XI.1971, 1 shell (MNRJ 3655), 2 shells (MNRJ 7571), 1 shell

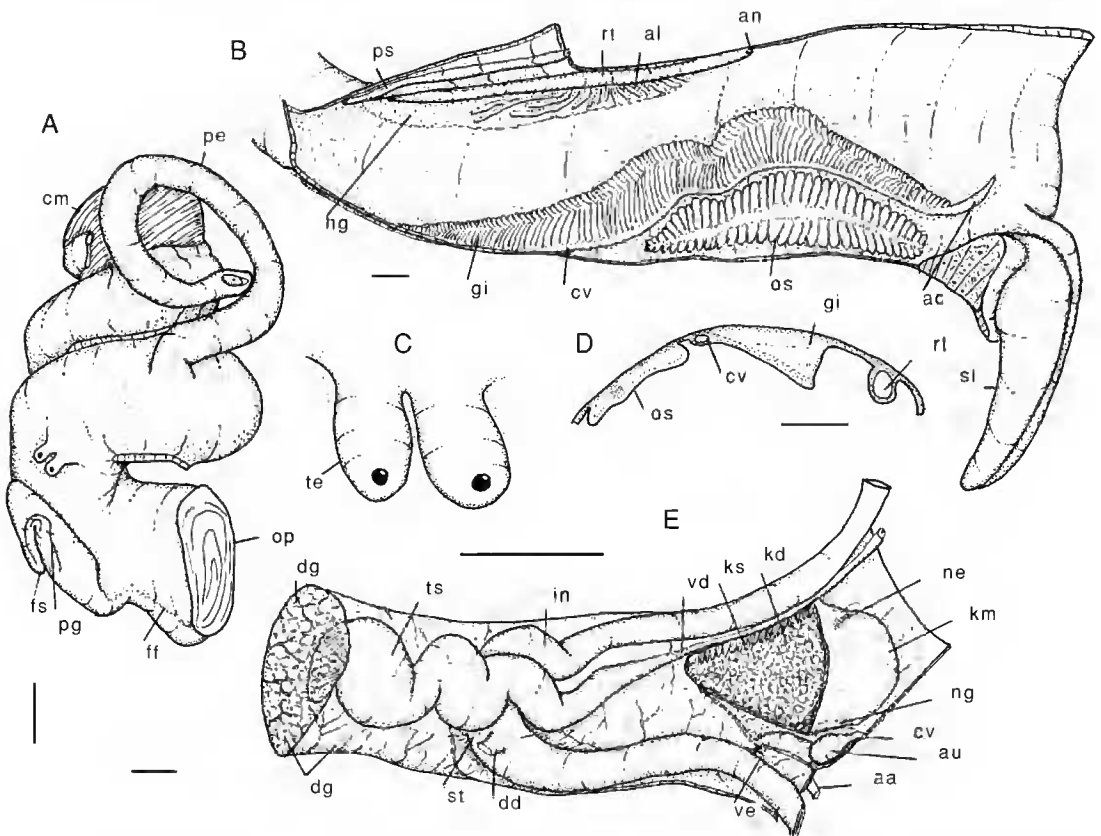
(MORG 39001), 1 shell (MORG 39002). — Off Itaipú, Niterói, 18 m (on sand): 1 shell (MORG 39000), 1 shell (MORG 22001). — Off Rio de Janeiro, 55 m (on sand), 1 shell (MORG 39003), 40-50 m, 1 shell (IBUFRJ 8918). — Off Juatinga, 40-50 m, 2 shells (MORG 39005). — Ilha Grande, RV W. Besnard, stn 350, III.1969, 1 shell (MZSP 25212). — Enseada Lopes Mendes, RV *Emília*, stn 262-263, 20.VII.1966, 1 shell (MZSP 25206). — Angra das Reis, RV W. Besnard coll., stn 352, 19 m, 16.III.1969, 1 ♂, 1 ♀ (MZSP 25211); stn 349, III.1969, 1 ♂ (MZSP 25213). — Same locality, RV *Emília*, stn 248, 29 m, 17.VII.1966, 1 shell (MZSP 25205); stn 142c, 10 m, 19.VI.1967, 1 shell (MZSP 25198); stn 266c, 22.5 m, 17.VI.1967, 1 shell (MZSP 28708); stn 172, 8.VII.1966, 1 shell (MZSP 25202); stn 173, 20.5 m, 22.VII.1966, 1 shell (MZSP 25201); stn. 266, 22.5 m, 20.VII.1966, 1 shell (MZSP 25207); stn 292, 25 m, 30.VII.1966, 1 shell (MZSP 25209); stn 289, 42 m, 30.VII.1966,

FIG. 25. — *Terebra spirosulcata* n. sp., anatomy: **A**, ♂ head-foot, mantle removed; **B**, pallial organs, ventral-internal view; **C**, detail of **A** in tentacle region; **D**, pallial cavity roof, transverse section of its middle region; **E**, last whorl of visceral mass and posterior part of pallial cavity, ventral view, part of digestive gland adjacent to stomach removed, kidney and pericardium opened, internal structures exposed. Scale bars: **A**, 1 mm; **B-E**, 0.5 mm.

1 shell (MZSP 25208); sn 176, 30.4 m, 26.VII.1966, 2 shells (MZSP 25203); sn 236, 16.2 m, 12.VII.1966, 1 shell (MZSP 25204).

São Paulo. Paratypes: Ubatuba, Lagoa Beach; 5 shells (MZSP 28707).

Santa Catarina. Paratypes: Campeche Island, in beach, II.1985, 1 shell (MORG 39004).

TYPE LOCALITY. — Brazil, Rio de Janeiro, off Ilha do Pai, 30-40 m depth (sandy).

DISTRIBUTION. — From Rio de Janeiro to Santa Catarina, Brazil.

HABITAT. — From 10 to 60 m depth, sandy substrates.

MEASUREMENTS. — In millimeters. Holotype MNRJ 3657; 26.2×6.4 . Paratypes MNRJ 7570, 24.6×5.7 ; MNRJ 3655, 26.9×6.6 ; MNRJ 7571, 29.4×7.0 , 18.8×4.6 ; MORG 39000, 26.8×6.0 ; MORG 39003, 23.1×5.8 ; MORG 22001, 20.7×5.4 ; MORG 32755, 24.0×6.5 ; MORG 39001, 11.1×3.0 ; IBUFRJ 8918, 23.0×5.9 .

REMARKS

This species was simultaneously discovered by Paulo Marcio Costa, Universidade Federal do Rio de Janeiro. For this reason, he is included as one of the authors herein.

DIAGNOSIS

SE Brazilian deep-water species with medium-sized shell. Sculptured with low axial undulations and narrow spiral furrows. Larger specimens with last whorl outstandingly large. Foregut with complete venom apparatus and a very long introvert.

DESCRIPTION

Shell (Fig. 1E, F)

Long, slender, turritiform, of medium size (about 40 mm high), up to fifteen almost flat to convex whorls, white cream, some specimens with brown axial blotches. Protoconch of 2.5 whorls, convex, smooth. Teleoconch glossy, sculptured mainly by very shallow axial ribs, almost undulations (Fig. 13C), uniformly spaced, about 23 on penultimate whorl, more prominent near upper suture; about eight spiral furrows on anterior (lower) two thirds of each whorl, rather equally

spaced, except the upper ones, which may be closer to one another than the lower ones. In larger specimens last whorl very large in relation to preceding whorls (Fig. 1E, F). Aperture simple, large; outer lip with cut edge; inner lip smooth, sigmoid. Canal short, open, curved.

Head-foot (Figs 25A, C; 26A)

Colour homogeneous cream. Head weakly differentiated from head-foot axis (Fig. 25A). Tentacles moderately developed, dorso-ventrally flattened, tip rounded, broad (Figs 25A, C; 26A). Eyes dark, located at tip of tentacles. Basal, proximal introvert aperture rather broad, transverse, anterior and ventral to tentacles. Foot of about half a whorl, without clear divisions; sole with folded borders. Furrow of pedal gland anterior. Columellar muscle of about 1.5 whorl, thick.

Operculum (Figs 3H; 25A)

Unguiculate, pale brown, nucleus terminal (Fig. 3H). Occupying entire shell aperture (Fig. 25A).

Mantle organs (Fig. 25B, D)

Mantle border simple, not pigmented. Siphon well-developed, pale cream in colour, borders smooth. Mantle cavity of about two whorls. Osphradium bipectinate, elliptical, long, about half of gill length; with several uniform filaments on both sides of osphradial ganglion; right filaments obviously larger than left filaments; each filament with smooth surface (not scalloped). Gill narrow and long, about eight tenths of pallial cavity length; anterior end rather far from mantle border; with only ctenidial vein present, in from of a small septum; filaments begin gradually at some distance from anterior end; each filament triangular, apex located at right; gill posterior end far from pericardium. Ctenidial vein narrow and uniform all along its length, except for its broader anterior extremity. A proportionally broad space between gill and rectum. Hypobranchial gland thin, small, located in posterior half of cavity, at left of rectum, pale cream. Anal gland with several slender, irregular acini immersed in right margin of hypobranchial gland close to rectum (Fig. 25B), purple; post-

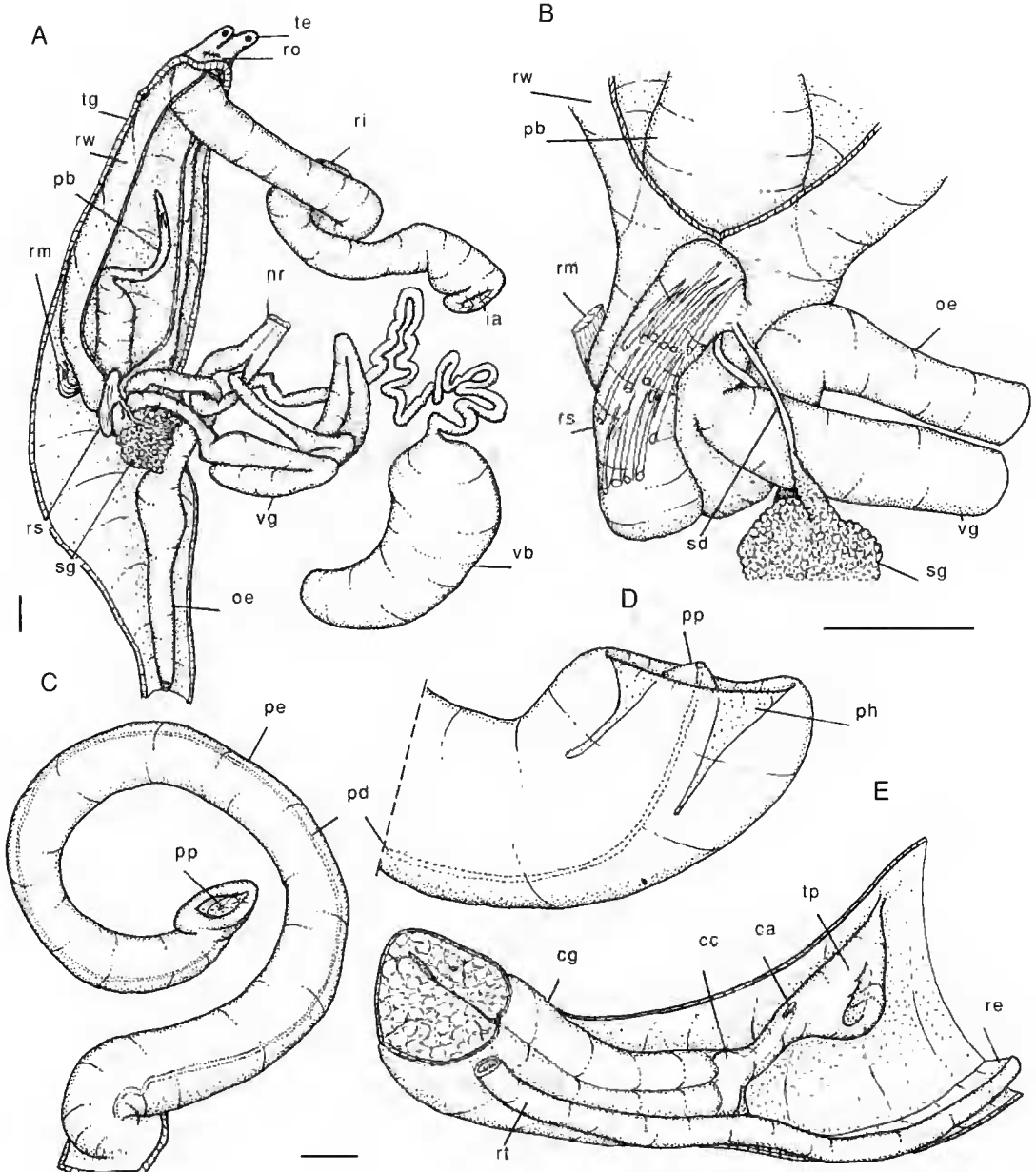


FIG. 26. — *Terebra spirosulcata* n. sp., anatomy; **A**, head and haemocoel, ventral view, foot and columellar muscle removed, rhynchodeal wall partially opened with introvert reflected outside; **B**, detail of posterior extremity of rhynchodeum and buccal mass, ventral view; **C**, penis, dorsal view; **D**, same, detail of its distal extremity as a transparent structure; **E**, pallial oviduct (posterior extremity damaged) and adjacent region of pallial cavity, ventral view. Scale bars: 0.5 mm.

erior acini longitudinally disposed. Pallial gonoducts run along right margin of posterior half of pallial cavity, partly connected to pallial floor. Rectum narrow, lying to left of pallial gonoducts;

in female gonoduct separates from pallial oviduct after capsule gland, runs in tip of a small septum (Fig. 26E: re), far from terminal pouch. Anus far from anterior extremity of pallial oviduct in

females or prostate in males; sessile, without papilla; located in about middle region of pallial cavity. Anterior half of pallial right margin without interior structures.

Circulatory and excretory systems (Fig. 25E)

Heart similar to those of preceding species. Kidney of almost half a whorl, flattened, located in right region of posterior limit of pallial cavity. Kidney with two thin glandular masses, separated by broad, high chamber. Dorsal glandular mass thin, white, bearing a mosaic of irregular acini, obviously thicker in anterior region. Ventral glandular mass very thin, bordering rectum, semi-transparent, bears several, uniform transverse folds. Nephridial gland narrow, white, triangular in section, bordering dorsal margin of membrane between kidney and pericardial chambers. Nephrostome a transverse slit in mid-right region of membrane between kidney and pallial cavity.

Digestive system

(Figs 6H, I; 7E; 8D, E; 25E; 26A, B)

Rhynchodeal introvert narrow and very long, about double length of rhynchodeal cavity length, coiled within rhynchodeal cavity, cylindrical (Fig. 26A), with thick muscular walls. Distal aperture of rhynchodeal introvert (rhynchostome) a small transverse slit; a thin sphincter preceding it. Internal rhynchodeal wall very thin, transparent, covering internal surface of anterior half of haemocoel (Fig. 26A, B), connected to it by small muscle fibres mainly located near rhynchostome. Proboscis conical, narrow distally, of about same length as rhynchocoel, its base connected by small muscle fibres in rhynchodeal wall and by retractor muscle; proboscis wall rather thin. Buccal mass spherical (Fig. 26B), with a long and broad buccal tube, double-walled, with organization similar to that of *H. cinerea*. Pair of retractor muscles also inserts in buccal mass lateral surface. Radular sac rather short, curved, with several radular teeth, opens sub-terminally in mid-ventral region of buccal mass. Radula of about twenty teeth, each tooth (Fig. 6H, I) hollow, broad, about 450 µm in length, section almost circular (but not altogether fused), base barbed, surface irregular (with

rather uniform, scale-like proximal half), narrows at tip; tip harpoon-like, with a narrow aperture. Salivary glands a pair of amorphous, white masses connected to each other; their ducts contour oesophagus and insert in anterior and posterior side of base of radular sac aperture. Venom gland very long and convolute (Fig. 26A), about half anterior and half posterior to nerve ring; proximal half of venom gland (Fig. 8D) broader and more flaccid than distal half, with thin glandular walls; distal half has thick glandular walls and a very narrow duct (Fig. 8E); inserts in buccal mass close to and to left of radular sac aperture. Muscular bulb rather long, elliptical, with broader proximal region; two muscular layers, internal layer thinner than half thickness of outer layer. A sketch of foregut structures shown in figure 7E. Internal surface of buccal mass similar to that of *H. cinerea*. Oesophagus long and narrow, with smooth internal surface. Stomach similar to those of preceding species (Fig. 25E). Duct to digestive gland single, located in mid-ventral region of stomach. Digestive gland of about 4.5 whorls posterior to stomach, beige. Intestine narrow, with thin walls, internal surface almost smooth; runs left and ventral to margin of kidney (Fig. 25E). Rectum and anus described above.

Genital system (Figs 25A, E; 26C-E)

Male. Testis in columellar side of visceral mass, sinuous, narrowing gradually anterior to stomach (Fig. 25E), iridescent white in this region. Visceral spermoduct appears as continuation of testis, very narrow, runs ventrally between rectum and kidney (Fig. 25E). Pallial spermoduct runs along right margin of pallial cavity floor (Fig. 25A), without development of clear prostate tissue. Penis very long, cylindrical, coiled (Fig. 25A); penis duct simple, very narrow, runs near left margin of penis (Fig. 26C). Penis distal end with a concavity turned to right (Fig. 26D), in its centre a large, broad papilla in which penis duct opens. Penis papilla about in centre of penis tip concavity.

Female. Posterior region of pallial oviduct not seen in detail in Figure 26E. Albumen gland short, of same width as capsule gland, from which it is difficult to separate. Capsule gland

long, broad, almost cylindrical, its glandular tissue suddenly finishes, leaving a small anterior hollow chamber; a narrow duct runs from this chamber anteriorly. Capsule gland aperture small, in posterior region of terminal pouch, turned to columella. Terminal pouch about half of capsule gland length and separated from gland by a narrow region; middle region broad, with a broad, longitudinal, shallow aperture.

DISCUSSION

The shell of *T. spirosulcata* specimens resemble that of *T. brasiliensis*, differing mainly by its larger size and by its narrow spiral furrows. These differences were noted by Bratcher & Cernoholsky (1987) who regarded them only as variation and growth effect. On the basis of soft part characters, however, no doubts persist of their specific separation. *T. spirosulcata* differs from *T. brasiliensis* mainly in having: (1) cephalic tentacles closer; (2) a complete proboscis (while in *T. brasiliensis* it is vestigial); (3) a complete venom apparatus (while *T. brasiliensis* has lost it); (4) absence of accessory proboscis structure; (5) penis longer, and (6) terminal pouch of females widely open. Matthews *et al.* (1975) also commented on and figured this species, calling it a probable variation of *T. doellojuradoi*.

Terebra sterigma n. sp. (Figs 12D; 13G; 14D, H)

TYPE MATERIAL. — Holotype: MNHN. Paratypes: 1 shell, MNHN; 1 shell, MZSP 28727. All these from type locality.

TYPE LOCALITY. — Brazil, Espírito Santo, off Regência, 19°34'S, 38°55'W, 340–360 m (RV *Marion-Dufresne*, MD55, sin CB92, V.1987).

ETYMOLOGY. — The specific epithet refers to the shell sculpture, which is mainly axial ribs, from Greek *sterigma* (poles).

DISTRIBUTION. — Known only from the type locality.

MEASUREMENTS. — In millimeters, followed by number of axial ribs and spiral nodes in penultimate whorl; holotype: 16.5 × 3.9, 25, 8; paratype: 16.7 (broken) × 4.1, 25, 8.

DIAGNOSIS

SE Brazilian deep-water species with medium-sized shell. Sculptured with many prominent axial ridges

REMARKS

Shell (Fig. 12D) long, slender, turritiform, of medium size (about 20 mm high), up to 14 whorls, homogeneous clear brown. Protoconch (Fig 14D) of two whorls, convex, smooth; junction with teleoconch obvious. Teleoconch sculpture lirate (Figs 12D; 14H), of many axial, orthocline ribs, uniformly spaced and close to one another, about 25 on penultimate whorl; spiral sculpture absent or only indicated by successive small, shallow nodes on axial ribs (about eight on penultimate whorl); a shallow subsutural furrow. Aperture simple (Fig. 13G); outer lip with cut-edge; internal lip sigmoid, smooth. Canal short, open, curved.

DISCUSSION

This species was first discovered by Dr. Bouchet (MNHN) and the specimens were kindly sent to be included in this study. *T. sterigma* differs from *T. doellojuradoi*, *T. crassireticula* and *T. leptapsis* by the absence of well-developed spiral ribs, by the broader shell, and, particularly from *T. crassireticula*, by the number of protoconch whorls (two rather than one).

DISCUSSION

The present discussion includes comparisons of the morphological characters of the species described here and also comparisons with other closer (conoideans) and more remote gastropods. The arguments presented are based on literature data and also on self-observed species [e.g., Cerithioidea, *Littorina flava*, Hydrobioidea (Simone & Moracchioli 1994; Simone 1995a), tonnids (Simone 1995b), several muricoideans such as *Buccinanops* sp. (Simone 1996), *Thalacra* (Simone 1995c), *Austromitra* sp. (Turner & Simone 1998, some papers still in press). Other self-observed conoideans are the turritid *Cochlespira* sp. (papers in press) and the conid *Conus bertarollae* Costa & Simone, 1997. This

discussion excludes those made by Taylor, Kantor & Sysoev (1993), except if there is any interesting comment. That paper is recommended as a complement to this discussion.

SHELL

The elongated, multispiral form of the terebrid shell is a long-known character of the family. *T. brasiliensis*, however, presents a form of adult shell similar to other species when they are immature, i.e., with proportionally few whorls and a large protoconch, combined with mature genital organs. Thus the term "paedomorphic" (i.e., young form) appears appropriate to define this character of *T. brasiliensis*.

Unlike the other terebrids, *T. taurina* possesses a well-developed, tall fold running down the entire middle region of the columella (Fig. 13D), evident until near the internal lip.

The number of protoconch whorls appears to be in general one whorl. In the present analysis the only species seen with more than one whorl was *T. crassireticula*.

HEAD-FOOT

The foot of *H. cinerea* combined interestingly a large foot size (more than half a whorl in length), with a reduced operculum. The larger size of the *H. cinerea* foot is possibly an adaptation to the high-energy environment it lives in.

All terebrids have a considerable reduction of the tentacles. In some species they can only be seen by means of a microscope. The eye position, on the other hand, appears to divide the terebrids into two groups: the *Hastula* species which have the eyes located in the tentacle bases, and the *Terebra* species which have the eyes in the tips of the tentacles (except for *T. gemmulata* with reduced eyes). *H. bacillus* (cf. Taylor & Miller 1990) also has basally placed eyes.

PALLIAL ORGANS

As in most other gastropods, the siphon of the terebrids has smooth margins, but *H. cinerea* has a series of papillae on the siphon border. Of the examined species, *H. cinerea* is the only one constantly exposed to intertidal waves. The papillae on the siphon border may be an adaptation to avoid sand pollution in the pallial cavity

(Fig. 2B). This adaptation is unnecessary in the other deeper water species. On the other hand, *H. bastata* has a pair of basal projections on the siphon (Fig. 9B), resembling those of the Volutidae (Muricoidea).

The osphradium is always well-developed in these predatory animals. In some species, it is even larger (in area) than the gill (e.g., *T. crassireticula*, *T. leptapsis*) or presents scalloped leaflets (e.g., *H. cinerea*, *H. bastata*). Reduction of the left filaments, found in *T. crassireticula*, *T. leptapsis* and *T. brasiliensis*, is normally associated with size reduction as, e.g., in Columbellidae (Muricoidea) (pers. obs.). These terebrid species are of small size.

The gill anterior extremity of the examined terebrids (except *T. crassireticula*) is raised, septum-like, and the gill filaments begin after a short distance. The presence of this small septum preceding the gill filaments appears to be a modification of the crenidial vein, but more detailed study is necessary to confirm that. However, the absence of this character in other families examined (even conoideans) indicates it may be another character limited to terebrids.

The long, digitiform glandular acini, of conspicuous purple colour, found in the right region of the pallial cavity is here called the anal gland, following the terminology of Marcus & Marcus (1960). Further research, however, appears necessary to determine its homology with the anal gland of the Muricidae. The terebrid anal gland appears to be a specialized region of the hypobranchial gland, rather than a structure associated with the anus, from which it is distantly separated in some species. Also, it is lacking in *T. crassireticula*, *T. leptapsis*, *T. brasiliensis* and *T. taurina*.

In females of *T. crassireticula* and *T. spirosculcata*, the end region of the rectum lies on an enigmatic septum, instead of directly connected to the mantle surface. This character is absent in males of the same species, and deserves investigation in immature females.

KIDNEY

Except for *T. brasiliensis*, all examined terebrids have a kidney comprising a broad chamber limited by two lobes, one lobe separate, attached to the rectum and the other flattened and dorsal.

An almost solid kidney (without large internal hollow chamber) appears to be more primitive, however some doubts exist with respect to the typical kidney of conoideans.

DIGESTIVE SYSTEM

The rhynchodeal wall in conoideans can be muscular or membranous. In the turrid *Cochlespira* and some Crassispirinae (Kantor *et al.* 1997) it is of the first type. Muscle fibres present in the rhynchodeal wall indicate some degree of contractile function. This state is not found among terebrids, of which the internal rhynchodeal wall is practically only a membrane, however, several other conoideans show this condition (Taylor *et al.* 1993). The terebrid rhynchodeal wall still has a thin layer of muscular fibres in the region near the retractor muscle of the proboscis (Fig. 8A).

The proboscis of the conoideans, called an intraembolic proboscis, has been regarded as an independent acquisition from those of other gastropods, particularly from other caenogastropods (Kantor 1990). On the other hand, recent papers on gastropod phylogeny show the conoideans as the last clade of the caenogastropods, with relationships with at least two clades of pleurembolic probosciferous animals such as muricoideans and cancellarioideans (Ponder & Lindberg 1996, 1997; Kantor 1996). With these data in mind, it is already possible to construct a relationship between the pleurembolic proboscis and the conoidean intraembolic one.

Furthermore, observing the structures of a complete foregut extracted from the examined species, more similarities with the pleurembolic proboscis appear. The rhynchodeal wall is a distinct membrane, connected with the internal surface of the haemocoel by several small muscle fibres, which vary in number according to species and to specimens; these small muscle fibres are in general more concentrated anteriorly, close to the rhynchostome. These muscles are easily cut in dissections and then the rhynchodeal wall becomes a free structure connected only by the rhynchostome. The rhynchodeal wall is continuous with the proboscis, i.e., the proboscis is not inserted in the haemocoel internal wall. The transition from the rhynchodeal wall to the pro-

boscis is noted by a sudden or sometimes gradual increase of the wall muscular tissue. The small muscle fibres which connect the rhynchodeal wall to the internal surface of the haemocoel are also generally concentrated at the transition from rhynchodeal wall to proboscis, forming a muscular ring as a base for these structures to work. From the internal surface of the proboscis, generally a pair of proboscis retractor muscles inserts, runs towards the posterior, crosses between the rhynchodeal wall-proboscis transition and the buccal mass, and connects in the lateral and ventral regions of the internal surface of the haemocoel just posterior to the buccal mass level.

The group of structures that compose the intraembolic proboscis (rhynchodeal wall, proboscis and its pair of retractor muscles) closely resembles the whole pleurembolic proboscis, from which it differs only by lacking muscular tissue in its outer wall (rhynchodeal wall) and by the short retractor muscles. With these arguments it is possible to offer another scenario for the evolution of the conoidean proboscis (see also comments on buccal mass and tube below): the conoidean ancestor was a pleurembolic probosciferous neogastropod; it lost the muscular tissue of the outer surface of its proboscis and shortened its retractor muscles, becoming the main protractible structure of the buccal mass part of the proboscis, and also acquiring a permanent rhynchodeal cavity where the prey was partly or wholly brought for initial digestion. In other words, the conoidean proboscis may be homologous to the buccal mass part of the pleurembolic proboscis (protractible) and the conoidean rhynchodeal wall is homologous to remaining regions of the pleurembolic proboscis (no longer protractible). These arguments are also corroborated by finds of muscular tissue in the rhynchodeal wall, mainly in its anterior extremity (close to the rhynchostome) and in its posterior extremity (close to retractor muscles) of examined terebrids. Moreover, *Cochlespira* still has the rhynchodeal wall entirely muscular (Simone *in press-a*), as well as some Crassispirinae (Kantor *et al.* 1997).

Parallel to conoidean proboscis evolution was that of the buccal mass and buccal tube. The buccal mass of examined species and most conoi-

deans (Taylor *et al.* 1993) is retained in the proboscis base even during protraction. This capacity is possible due the elongation of the buccal tube, which connects the buccal mass at the base of the proboscis with its tip. In observed terebrids and in *Conus bertarollae*, the buccal tube is not only long, but also double-walled. Its outer wall is in general thicker and muscular. Its internal wall is in general thin and with a glandular mucous epithelium, continuous with that of the buccal mass. It is possible that both walls of the buccal tube are connected to each other, and their separation is an artifact of the fixation; no living specimen was, however, dissected for confirmation.

A scarcely muscular rhynchodeal wall, the proboscis (or buccal mass part of the proboscis) as the main protractible structure, and the buccal mass situated in the proboscis base, connected with its tip by a long buccal tube, are not characters exclusive to the conoideans. At least, two muricoidean taxa developed convergently a very similar proboscis-buccal mass complex, such as the olivid *Amalda* (Kantor 1991) and the costelariid *Austromitra* (Turner & Simone in press).

The rhynchodeal introvert is a specialized tube of the anterior extremity of the foregut, inserted in the rhynchostomal region of the rhynchodeum, and can be retracted within it completely. Although double-walled, one wall does not glide over the other during protraction, instead the entire wall is evaginated and protracted, as a whole. This is observed in several specimens preserved with the introvert only partially protracted. This structure appears to be another terebrid character. The introvert is very long, i.e., as long as, or longer than the remainder of the rhynchodeum, in some species (*T. spirosulcata*, *T. gemulata*, *T. brasiliensis*). In other species, such as *T. gemmulata*, only the introvert is present, and most other foregut structures, including the proboscis and venom apparatus, have been lost. However, the large increase in the introvert is not necessarily accompanied by loss of the proboscis, as shown in *T. spirosulcata*. Other comments on the introvert are found in Taylor *et al.* (1993: 128).

A terminological problem was noted in the introvert, as both its extremities, the distal and the

proximal ends, could be called a rhynchostome. When it is extended, the distal aperture works as the rhynchostome, whereas when it is in the retracted position, the basal, proximal aperture performs this function (as observed in some specimens, the proboscis can protract without necessarily the protraction of the introvert). In the present paper, the recommendation of Dr Taylor (pers. comm.) is followed, using the term rhynchostome for the distal, apical introvert aperture.

Figure 7A shows a schematic synopsis of terebrid foregut structures, in ventral view, based on the Brazilian species examined, including the accessory proboscis structure (ap). This picture was obtained after detailed analysis of the examined species from dissections and serial sections, results shown in several figures through this paper and summarized in Figure 7B-G (these in dorsal view). These figures were inspired by those in the current literature (e.g., Taylor *et al.* 1993: figs 25, 26). The supposition of a close relationship between the intraembolic conoidean proboscis and the pleurembolic proboscis of its relatives (e.g., Muricoidea and Cancellarioidea) is summarized in Figure 27. Note, again, that the conoidean proboscis appears to be homologous to the buccal mass part of the pleurembolic proboscis, and the rhynchodeal wall of conoideans appears to be homologous to the remaining regions of the pleurembolic proboscis. The polyembolic proboscis, found in some conoideans such as *Terebra brasiliensis* and *T. gemmulata* represents, as noted Miller (1989) and Taylor *et al.* (1993) a gear development of the introvert accompanied by reduction of the proboscis and other structures of the buccal mass.

A pair of very long, well-developed accessory salivary glands is present in *H. bastata* and *T. taurina*. However, in *H. bastata* one is far from the other, inserted on the opposite side of the proboscis base (each one close to a retractor muscle), while those of *T. taurina* are inserted close to each other in the buccal mass. The homology of these accessory salivary glands with those of the other neogastropods is a matter for further studies. As is normal for probosciferous prosobranchs, most terebrids possess a pair of strong retractor muscles at the base of the proboscis. However,

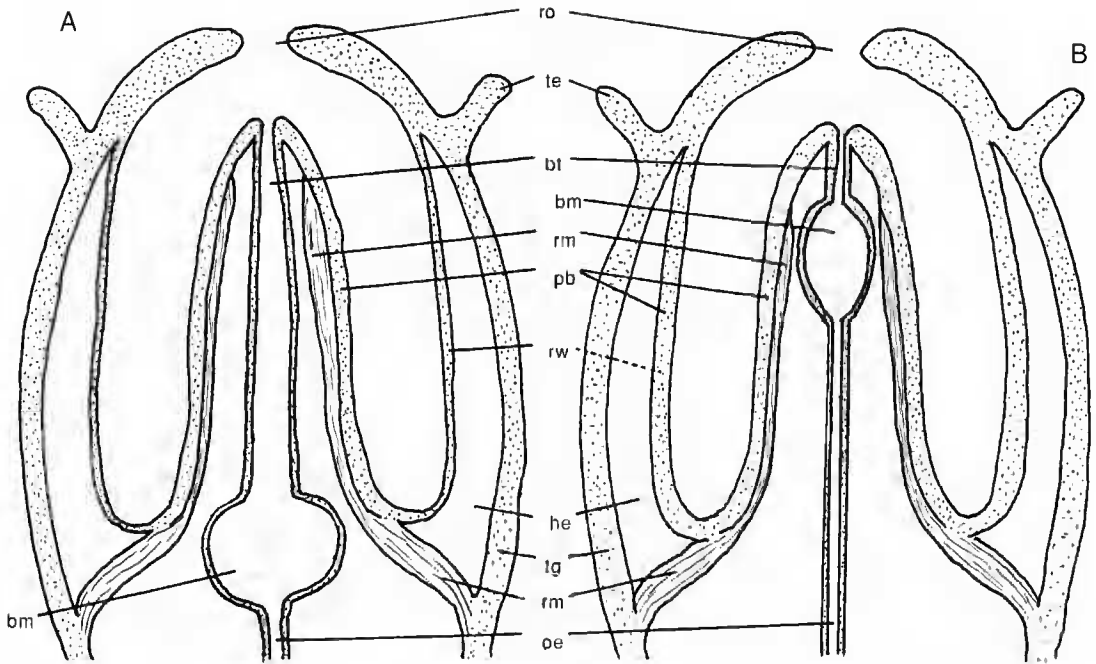


FIG. 27. — Schematic representation of transverse (frontal) section of head, not to scale nor proportions, showing the similarities between the conoidean proboscis (A) with the retracted pleurembolic proboscis of, e.g., a muricoidean (B). Note that the homology of each structure can be suggested. The rhynchodeal wall (rw) of conoideans is scarcely muscular (except in the turrid *Cochlespira*) and may be homologous the outer wall of the pleurembolic proboscis (indicated by dotted line). The conoidean buccal mass is basal, while it is apical in muricoideans, but both groups have exceptions to this state. See text for more explanations.

T. crassireticula, *T. leptapsis*, *T. brasiliensis* and *T. taurina* possess several small pairs, distributed around the basal region of the proboscis, connecting it with the adjacent region of the internal surface of haemocoel. Some fibres of the retractor muscles also are inserted into the rhynchodeal wall and buccal mass.

The accessory proboscis structure is another enigmatic character of terebrids, well-commented on by Taylor *et al.* (1993: 129) and regarded by them as a family synapomorphy (shared with its sister-taxon Pervicaciinae). Due to its presence in only some terebrids (e.g., the examined *T. crassireticula*, *T. leptapsis* and *T. brasiliensis*), while others (and other conoideans) have no vestiges of this accessory structure, three main conclusions are possible: (1) it appeared in the terebrid ancestor and is secondarily lost in several members of the group; (2) it appeared only once in terebrids and is a synapomorphy of a subgroup; (3) it

appeared several times independently in terebrid species. That the last possibility is the most likely is corroborated by the high degree of variation of this organ, which in some species is a simple projection, while in others it is very complex and branched. On the other hand, it always appears in the same location (left side of rhynchodeal wall) and has a similar structure (muscular in the centre, glandular at the periphery with sensory receptors). This suggests homology rather than convergence. This question may only be resolved after further studies.

Most terebrids, like other groups, possess female pallial gonoducts closely attached to the rectum, but in *T. gemmulata* and *T. taurina* the rectum is deflected in the middle or posterior region of the oviduct, so the pallial gonoduct no longer lies near the rectum.

The terebrids (except *H. bastata*) show an interesting tendency for a posteriorly located anus, far

from the mantle border. This keeps a relatively long region at the right of the pallial cavity free of visible structures and may be another terebrid character. The anal papilla is also found in *Cochlespira*, and its presence in terebrids may be plesiomorphic. However, the anal papilla appears to be lost in *T. brasiliensis*, *T. spirosulcata*, and *T. gemmulata*.

GENITAL SYSTEM

The testis-seminal vesicle complex and the ovary of the terebrids taper gradually until they unite with the gonoduct. This condition differs from other groups in which there is normally a sudden constriction separating the two regions. However, this character is still obscure among other conoideans.

The prostate location in most terebrids is in the pallial cavity as in most caenogastropods. However, two species are exceptions. In the case of *T. gemmulata*, the prostate is located in the anterior region of the visceral mass, by the side of (and compressing) the kidney. In the case of *T. spirosulcata*, no differentiated prostate is present, it is possibly distributed as a thin glandular tissue along the pallial spermoduct.

Some muscles of the penis base, protruding into the haemocoel, are clearly visible in several caenogastropods, but in the case of *H. hastata*, these muscles are much more complex and enlarged, and when fully developed, displacing the foregut structures to the left. Most of the terebrids have a broad papilla in the penis tip, but it is absent in *T. taurina*. Something similar to this broad papilla is also found in the turrid *Cochlespira* and it may be a basal character of the conoideans.

The ingesting gland of the pallial oviduct is normally located between the albumen and capsule glands in the neogastropods. This condition is also found in the terebrids. However, *H. hastata*, *T. crassireticula* and *T. brasiliensis* have the ingesting gland posterior to the albumen gland.

A terminal pouch with a large aperture is found in the examined terebrids (except *T. crassireticula*) and also in the turrid *Cochlespira*. It may be another character of the superfamily. *T. crassireticula* has probably lost this structure. *T. brasiliensis*, on the other hand, possesses a very narrow anterior aperture of the terminal pouch, with a deep,

blind sac duct. This condition resembles the bursa copulatrix of several Muricoidea and of *Conus bertarollae* Costa & Simone, 1997, from which the terminal pouch may have evolved; if so, the *T. brasiliensis* condition could have assumed the plesiomorphic condition, which would be another indication of pedomorphosis.

SPECIES GROUPS

The terebrids, in the same way as several other molluscan groups, have revealed that small differences in shell characters, which might be regarded as variation, may indicate deeper differences in internal anatomy, for example, in *T. brasiliensis* and *T. spirosulcata*. It is interesting to note, however, that there are several "species groups" among Brazilian terebrids, i.e., species with greatly similar shell characters. This is the case of, e.g., the *H. cinerea* "group", which includes intertidal species such as *H. salleana* (Deshayes, 1859) and *T. imitatrix* Auffenberg & Lee, 1988; the *T. doellojuradoi* "group", which includes deep water, reticulate-sculptured species such as *T. crassireticula*, *T. leptapsis* and *T. stierigma*; and the *T. protexta* (Conrad, 1846) "group", which includes spirally grooved species such as *T. riosi* Bratcher & Cernohorsky, 1985 and *T. spirosulcata*. Perhaps in the future, when more species are known in more anatomical detail (mainly the internal anatomy), these similarities could be better analysed.

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